AN AUTECOLOGICAL STUDY ON *HYDROMYZA LIVENS* (FABRICIUS) (DIPTERA, SCATOMYZIDAE), A FLY ASSOCIATED WITH NYMPHAEID VEGETATION DOMINATED BY *NUPHAR*[1])

by

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ABSTRACT

The life history and autecology of the fly *Hydromyza livens* (Fabricius) were investigated in detail in two Dutch waters. Special attention was paid to its effects on and interrelations with vegetation dominated by *Nuphar lutea* (L.) Sm. The food plants, geographical distribution, aspects of population dynamics and the morphology of *H. livens* are described and discussed.

Investigations have been made on general behaviour, feeding behaviour, spatial occurrence, sexual behaviour, sex ratio, oviposition, mortality and predation of the adults. The function of the chorion of the egg is discussed. Some experiments have been carried out to study the development of the eggs in relation with humidity, oxygen and temperature. The process of hatching, feeding behaviour, mine patterns, the effect of temperature on feeding behaviour and the mortality of the larvae are described. Data are given of the position in the leaf stalks, emergence and hibernation of the pupae.

The life history of *H. livens* is compared with that of *H. confluens* Loew, a species bound to *Nuphar* in North America.

INTRODUCTION

Nymphaeid vegetations, which are very common and show an optimal development in The Netherlands, have been studied by us during several years. Nymphaeids are aquatic plants with floating leaves, which root in the bottom and have flowers above or floating on the water surface. Because of their structure they have an important function as a habitat for semi-aquatic insects.

The species *Hydromyza livens* (Fabricius, 1794) (syn. *Musca livens* Fabricius, 1794, and *Nupharia rivularis* Robineau-Desvoidy, 1830) of the dipteran family Scatomyzidae (syn. Cordyluridae, Scatophagidae) is such an insect occurring abundantly on the nymphaeids studied, especially on *Nuphar lutea* (L.) Sm. The larvae of most species belonging to this family live in dung; only a few genera are known to mine in leaves or petioles of plants (Sack, 1937). According to Hering (1926) the larvae of most *Hydromyza* species mine the leaves and/or petioles of Liliaceae and Orchidaceae.

Hydromyza livens, however, can complete its whole life cycle on *Nuphar lutea* (Nymphaeaceae), one of the nymphaeid species of which the structure and function is a subject of investigations in our laboratory. The larvae of *H. livens* mine the floating leaves of *Nuphar*. By their consumption of living plant tissue, the larvae are an important link in the grazer food chain and decomposition processes connected with *Nuphar lutea*. Because of our interest in these interrelations the life history and habits of *H. livens* were studied in detail and a review was made of the literature.

Furthermore the results of our study could be compared with those of Welch (1914, 1917) who studied the North American species *H. confluens* Loew, 1863, of which the life history and habits resemble those of *H. livens* in many ways.

DESCRIPTION OF THE STUDY AREAS

Most observations have been made in the Oude Waal near Nijmegen (municipality of Ubbergen, Province of Gelderland); some additional observations have been made in the Haarsteegse Wiel (municipality of Vlijmen,

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[1]) Contribution no. 19 of the Nymphaeid Project.

Province of Noord-Brabant). In both water bodies pure stands of *Nuphar lutea* occur. The waters differ, however, in their dimensions, water quality and bottom composition.

The Oude Waal (fig. 1) is an old river branch cut off from the river Waal, where extensive nymphaeid vegetation dominated by *Nuphar lutea*, *Nymphaea alba* L. and *Nymphoides peltata* (Gmel.) O. Kuntze occur. It consists of a large shallow water body, 1 km in length and about 250 m wide, and three interconnected ponds (fig. 1, D, E and F). The depth of the large shallow water body varies from 0.5 to 1.5 m; in the dry summer of 1976 it became almost completely dry. About once every two years the area is flooded in winter or spring by water from the river Waal; summer high waters occur only occasionally. The depth of the three interconnected ponds increases towards their centres to 2.5, 5.5 and 5.5 m, respectively (D, E and F). The bottom of the Oude Waal consists of a pattern of clay and sand, sometimes mixed, covered by a sapropelium layer of varying thickness.

The Haarsteegse Wiel (fig. 1) originated from two, but not simultaneous, bursts in the dike of the river Meuse. This water body has a surface area of 17.9 ha (44.2 acres) and a maximum depth of 17 m. The nymphaeid vegetation dominated by *Nuphar lutea* and *Nymphaea candida* Presl, is almost completely restricted to the southern and western parts of the lake, where they are sheltered against wave- and wind action. The bottom of the Haarsteegse Wiel consists mainly of sand (wash-over deposits), but where nymphaeids grow there is a layer of sapropelium, becoming thicker towards the littoral border. The hydrology of the lake is dependent on rain and ground water only; the water-level shows only small fluctuations.

Apart from the two described areas of investigation several waters in The Netherlands with vegetation dominated by *Nuphar* have been visited and checked for floating leaves with mines of the larvae of *H. livens*.

GEOGRAPHICAL DISTRIBUTION AND FOOD PLANTS

The ecological distribution of *H. livens* is mainly governed by its affinity for the food plants on which the larvae feed and on which they can complete their life-cycle.

In table 1 a literature review is given of the food plants of the larvae of *H. livens*. According to most authors the larvae mine in the leaves
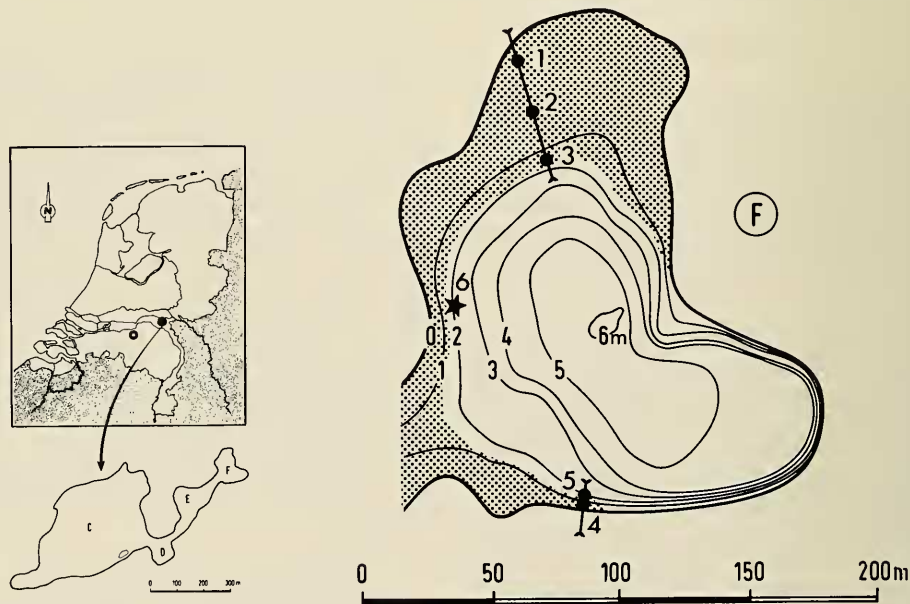

Fig. 1. Left side: the location of the areas studied in The Netherlands (open dot: Haarsteegse Wiel, closed dot: Oude Waal). Right side: bathymetric map of pond F of the Oude Waal, showing the nymphaeid beds (dotted area), the situation of transects studied in the *Nuphar* zone and the isolated *Nymphaea* bed (indicated by an asterisk).

Table 1. Review of the food plants of *H. livens* as mentioned in the literature.

Taxon	Author
Nymphaeaceae	Collin, 1958
Nymphaea	Wesenberg-Lund, 1943
Nymphaea alba L.	De Meyere, 1940
Nuphar	Hackman, 1956; Vockeroth, 1978
Nuphar lutea (L.) Sm.	De Meyere, 1895; Eberle, 1943;
	Gercke, 1877; Brauer, 1883;
	Hendel, 1928; Gaevskaya, 1966;
	Grünberg, 1910; Hering, 1926;
	Heslop-Harrison, 1955;
	Monchadskii, 1940; Sack, 1937; Seguy, 1934;
	Schütte, 1921; Van der Velde, 1978;
	Van der Velde et al., 1978
Nuphar pumila (Timm) DC.	Heslop-Harrison, 1955
Nuphar × *intermedia* Ledeb.	Heslop-Harrison, 1955
Caltha palustris L.	Gaevskaya, 1966; Monchadskii, 1940

and petioles of *Nuphar lutea*. This is confirmed in the present study; in all investigated Dutch waters with *Nuphar* stands floating leaves with mines of *H. livens* larvae were found. Heslop-Harrison (1955) mentioned *H. livens* larvae also from the leaves and petioles of *Nuphar pumila* (Timm) DC. and *Nuphar* × *intermedia* Ledeb. (= *N. lutea* × *N. pumila*). They were also found by us in floating leaves of *N.* × *intermedia*. It can be concluded from these data that all European *Nuphar* species are adequate food plants for *H. livens*. In the botanical garden of Haren (State University of Groningen, The Netherlands) the second author of this paper observed floating leaves of the North-American *Nuphar advena* Ait. with mines of *H. livens*. The occurrence of *H. livens* in America has not been reported.

In the literature there is some misunderstanding concerning the plant species on which *H. livens* can complete its life-cycle. De Meijere (1940) reported the occurrence of *H. livens* larvae in floating leaves of *Nymphaea alba*; in his paper, however, a drawing of a *Nuphar* leaf with mines of *H. livens* is given. In Wesenberg-Lund's "Biologie der Süsswasserinsecten" (1943) an obscure picture of *Hydromyza* mines in a so-called *Nymphaea* leaf is shown. Eberle (1943), however, who transplanted *Hydromyza* larvae from *Nuphar* leaves to *Nymphaea* leaves, and also to other *Nuphar* leaves, concluded that the transplanted larvae fail to develop in floating leaves of *Nymphaea*. We confirmed this in the laboratory for transplanted larvae in leaves of *Nymphaea alba* and *Nymphaea candida*. We never observed *Hydromyza* larvae in *Nymphaea* leaves.

According to Gaevskaya (1966), Monchadskii (1940) reported the occurrence of *Hydromyza* mines in leaves of *Caltha palustris* L.; this fact, however, is neither confirmed by other literature sources nor observed by the authors of the present paper.

Therefore, it can be concluded that in Europe *H. livens* is strictly bound to *Nuphar* species.

In the Limnofauna Europaea, Vockeroth (1978) reported several distribution areas for *H. livens* (see fig. 2), viz.:

(A) Areas with real records: the western secondary mountain chain (8), the central secondary mountain chain (9), the western lowlands (13), the central lowlands (14), Ireland (17) (Coon River near Partry, North of Lough Mask, 3 July 1982 on *Nuphar lutea* (L.) Sm. (G. van der Velde), the United Kingdom (18), Northern Sweden (22), Taiga (23), Uzbekistan, Siberia;

(B) Areas in which *H. livens* is expected to occur: the Alps (4), the Carpathians (10), the Hungarian lowlands (11), the Baltic Province (15), the eastern lowlands (16);

(C) An area in which *H. livens* does absolutely not occur: Iceland (19).

The distribution of *H. livens* does not extend beyond the confined distribution of the genus *Nuphar* in Europe. In fig. 2 both the geographical distribution of *Nuphar* (according to Meusel et al., 1965) and *H. livens* (according to Vockeroth, 1978) are compared. Both distribution areas coincide nearly perfectly. When considering fig. 2, the statement in the Limnofauna Europaea that *H. livens* does not occur in Iceland (19) is quite obvious, because *Nuphar* does not occur there either. On account of the geo-

Fig. 2. Map of the European distribution of both the genus *Nuphar* (dotted areas) (modified after Meusel et al., 1965) and *H. livens* (areas with numbers according to Limnofauna Europaea).

graphical distribution of *Nuphar*, *H. livens* might also be expected to occur in other regions such as Italy, the Balkans and Norway.

DEVELOPMENT IN TIME

In order to obtain an idea of the population dynamics of *H. livens* the occurrence in time of adults and larvae was quantified in various ways. Both the larval and adult stage can be easily recognized in the field. Adult *H. livens* can be found on the upper side of the nymphaeid floating leaves; the flies are not adapted to walking over the water surface, they have to fly from leaf to leaf. To quantify adult *H. livens* in time the insect-lime method was used (adhesive or sticky trap).

The mine tracks of the larvae of *H. livens* in the floating *Nuphar* leaves can be easily recognized and counted. To quantify the larvae and the number of affected floating leaves in time, the leaf-marking method was used.

The quantitative data of adults and larvae are

dealt with together in order to maintain to overall picture of the various generations of *H. livens* per year.

The insect-lime method. — Each week, from June until October, 1977, six undamaged floating leaves (five of *Nuphar lutea* and one of

Fig. 3. Adhesive trap (for explanation, see text).

Nymphaea alba) of the same size were gathered in the Oude Waal, pond F, and covered with insect-lime (Tangletrap or Stikem), which has no odour and consequently does not attract or repel the insects. These leaves, of which the petioles were removed, were attached onto six other floating leaves and then protected from predation by birds by wire netting (with meshes of 3 cm) which was supported by cork floaters (fig. 3). The wire netting with cork floaters was attached with a string to the petiole of the supporting leaf. After 24 hours these leaves were taken to the laboratory in plastic bags, so that the catch remained as undamaged as possible. The fauna was washed from the floating leaves with refined petrol and then fixed in 70% alcohol.

The leaves were laid out in transects from the littoral border vegetation to the open water, so that the distribution of the animals over the entire nymphaeid zone could be studied (see section on spatial occurrence on the nymphaeids, further below).

Leaf-marking method. — During two years (1976 and 1977) floating leaves and flowers of *Nuphar lutea* have been marked with 12 mm Rotex-tape on which a number was printed with a Universal 12 printer. One end of the tape was fixed around the petiole by means of a staple and the other end was drawn through the leaf-sinus and then bent over the leaf surface like a flag so that it could be easily read (fig. 4).

One plant forms too many leaves to follow the development in detail so that plots of one square metre were made with frames of PVC tubes. The perforated tubing was sunk into the water and held at approximately 15 cm depth by using a string-corner attachment to cork float-

ers. Each frame was anchored (Van der Velde, 1980). Observations and marking of newly unrolled leaves took place every week during the season. The marking of floating leaves made it possible to study the numbers of mines and the numbers of affected leaves per plot per time. Temperatures of air and water were read regularly.

Results. — In fig. 5 the leaf-marking observations for 1976 in the Oude Waal are presented; the summer of that year was characterized by a longlasting drought resulting in the emergence of parts of the *Nuphar* vegetation.

The numbers of mines, the numbers of affected leaves, and their percentages of the total numbers of floating leaves per plot, show the same tendency (fig. 5). The number of mines and affected floating leaves of *Nuphar* per plot remained relatively low in the months of May, June and July, while at the end of August and in the beginning of September the numbers of larval *H. livens* clearly reached their maximum. Also the quantity of mines per floating leaf was at its maximum in this period (fig. 5).

Figs. 6 and 7 present the data of 1977 in the Oude Waal (marking-method and insect-lime method) and the Haarsteegse Wiel (marking-method). The summer of 1977 was quite normal without droughts. At the end of May and the beginning of June small numbers of *H. livens* larvae occurred in both waters. The quantity of affected leaves reached a maximum in the Haarsteegse Wiel from the last week of July until the second half of September. The larval population of *H. livens* in the Oude Waal was also large in this period with a small peak at the end of July and an absolute maximum in the last week of August.

The data concerning the adult stage of *H. livens*, obtained with the insect-lime method, are summarized in table 2 and fig. 6. Among the total catch of approximately 23,158 specimens (of which 99.4 Hexapoda and 0.6% Arachnida) 1,055 specimens were adult *H. livens*, i.e. 4.56% of the total catch (see for some other results Van der Velde (1978), Van der Velde & Brock (1980) and Van der Velde (1980)). The highest numbers of adult *H. livens* were caught from 18 August until 8 September.

Discussion. — With respect to the insect-lime method one should keep in mind that the result is not only dependent on the size of the *H. livens* population, but also on changes in the activity pattern of adult *H. livens* as, for example, caused by weather conditions. This is also valid

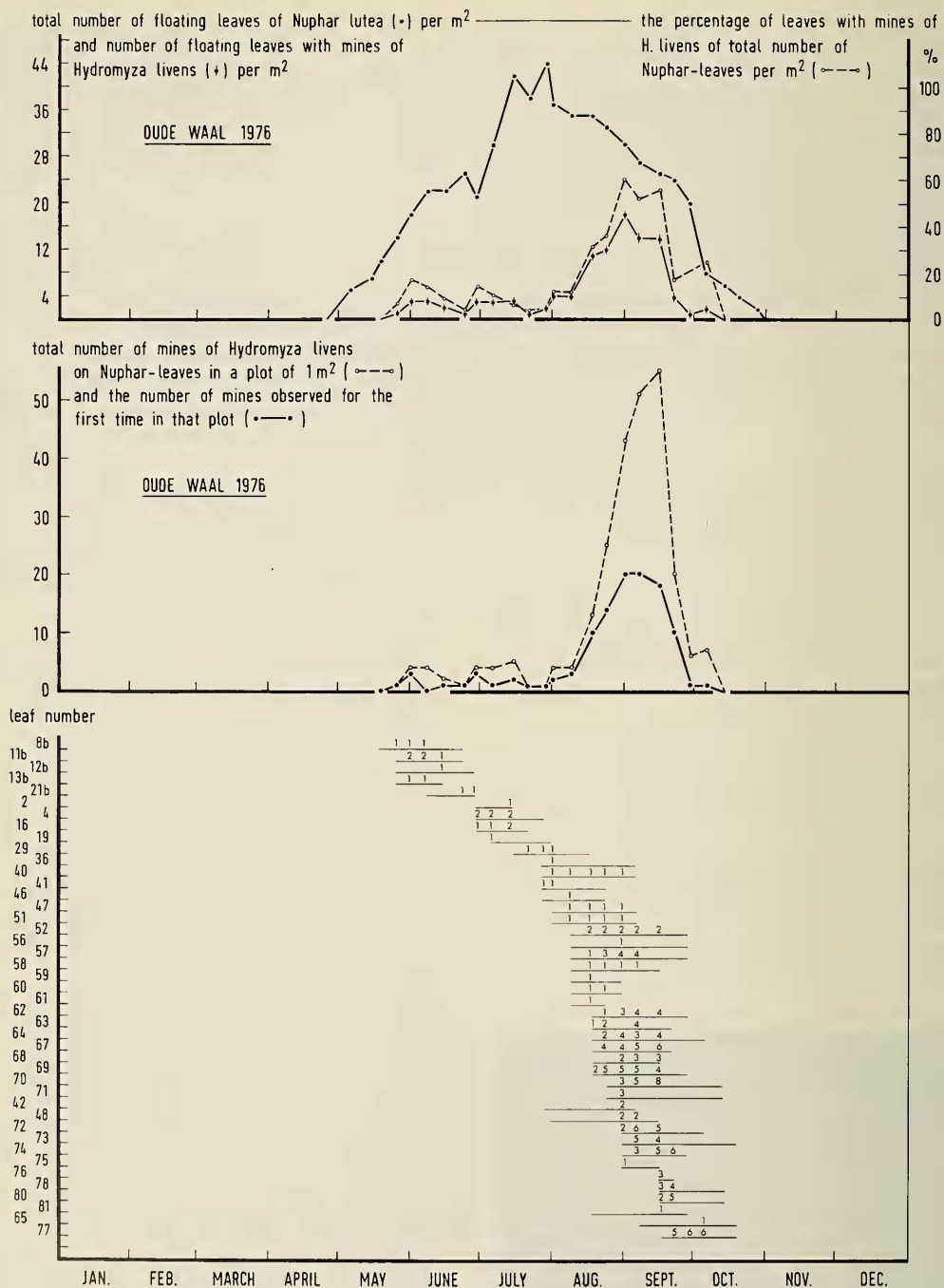Fig. 4. A *Nuphar* leaf, marked with rotex tape (leaf-marking method).

Fig. 5. Above: Total number of *Nuphar* leaves and absolute numbers and percentages of *Nuphar* leaves affected by *H. livens* per m², during 1976, in the Oude Waal. Middle: Total number of *Hydromyza* mines in a 1 m² *Nuphar* plot and the number of mines observed for the first time in that plot, during 1976. Below: The presence in time of all *Nuphar* leaves which were affected by larvae of *H. livens* in a plot of 1 m². Each line represents the occurrence in time of an affected floating leaf. The numbers above these lines represent the numbers of mine tracks of *H. livens* in these leaves.

Table 2. Number of adult *H. livens* caught with insect-lime on floating leaves from 16 June until 29 September, 1977. For the localities of the different leaves see fig. 1 and the text.

Date 1977	Leaf number	Number of *H. livens* caught							Total number of insects and spiders caught	% *H. livens* of total catch
		1	2	3	4	5	6	Total		
		Broad *Nuphar* zone			Narrow *Nuphar* zone		*N. alba*			
16-VI		—	—	—	—	—	—	—	1401	—
23-VI		1	—	—	—	—	—	1	715	0.14
30-VI		1	—	2	—	3	1	7	1195	0.59
8-VII		3	7	12	3	7	2	34	2234	1.52
12-VII		7	7	2	6	7	—	29	3168	0.92
21-VII		7	12	4	9	14	2	48	2287	2.10
28-VII		8	7	4	6	—	1	26	1284	2.02
5-VIII		15	9	6	—	5	3	38	1580	2.41
12-VIII		7	17	20	—	7	10	61	1578	3.87
18-VIII		54	22	66	15	20	20	197	1322	14.90
25-VIII		33	88	64	29	14	13	241	1303	18.50
1-IX		12	13	54	2	33	12	126	1421	8.87
8-IX		16	68	66	14	21	5	190	1876	10.13
15-IX		7	11	15	3	3	5	44	762	5.77
22-IX		—	4	9	—	—	—	13	584	2.23
29-IX		—	—	—	—	—	—	—	448	—
Total number per leaf		171	265	324	87	134	74	1055	23158	4.56

for the other insects, so that percentages of *H. livens* with respect to the total catch per date have been calculated (table 2). The absolute numbers and percentages showed the same trend, so that the catch gives a realistic picture of the adult population development in time.

When considering figs. 5, 6 and 7 it is clear that the development of the population of both adult and larval *H. livens* is correlated with the development of the floating leaves of *Nuphar lutea*. The first mine tracks on the floating leaves can be recognized early in the growing season of *Nuphar*, and at the end both the total numbers of floating leaves per plot and the numbers of *H. livens* diminish with the same tendency.

From the data obtained it can be concluded that *H. livens* has two or three generations per year in the studied waters. The third generation of the year before, which has hibernated in the pupal stage, occurs in May and June and the number of animals is small. The experiment with the insect-lime started too late to show this generation in the adult stage; adult flies, however, were caught by us with a hand-net in this period.

In the Oude Waal adults of *H. livens* were observed in 1975 from 5 June until 29 September, and in 1977 from 23 May until 22 September. The first generation in the Oude Waal in

1977 was present as larvae in May and the first week of June; adults of this generation were present at the end of June and in July. The maximum of adults was on 21 July. The second generation was present as larvae in the second half of July and the beginning of August. The maximum of adults was reached on 25 August. The third generation was present as larvae at the end of August and the first half of September. This generation hibernates as pupa and the adults of this generation were present in the next spring.

The data from the Oude Waal in 1976 do not indicate so clear the occurrence of three generations, that year, however, was characterized by a longlasting drought. This may have caused the establishment of only a minor second generation.

The population data from the Haarsteegse Wiel show two peaks (fig. 7), a minor one in the second half of May and the first weeks of June (first generation) and a large one in the second half of July, August, September and October. That the second peak is spread out over such a long period probably indicates that the second and third generation overlap, resulting in one broad peak only, as shown in fig. 7.

It can be concluded from the numbers of affected leaves per plot that in the Oude Waal in 1977 the second larval generation is ca. 6 times larger than the first generation while the third
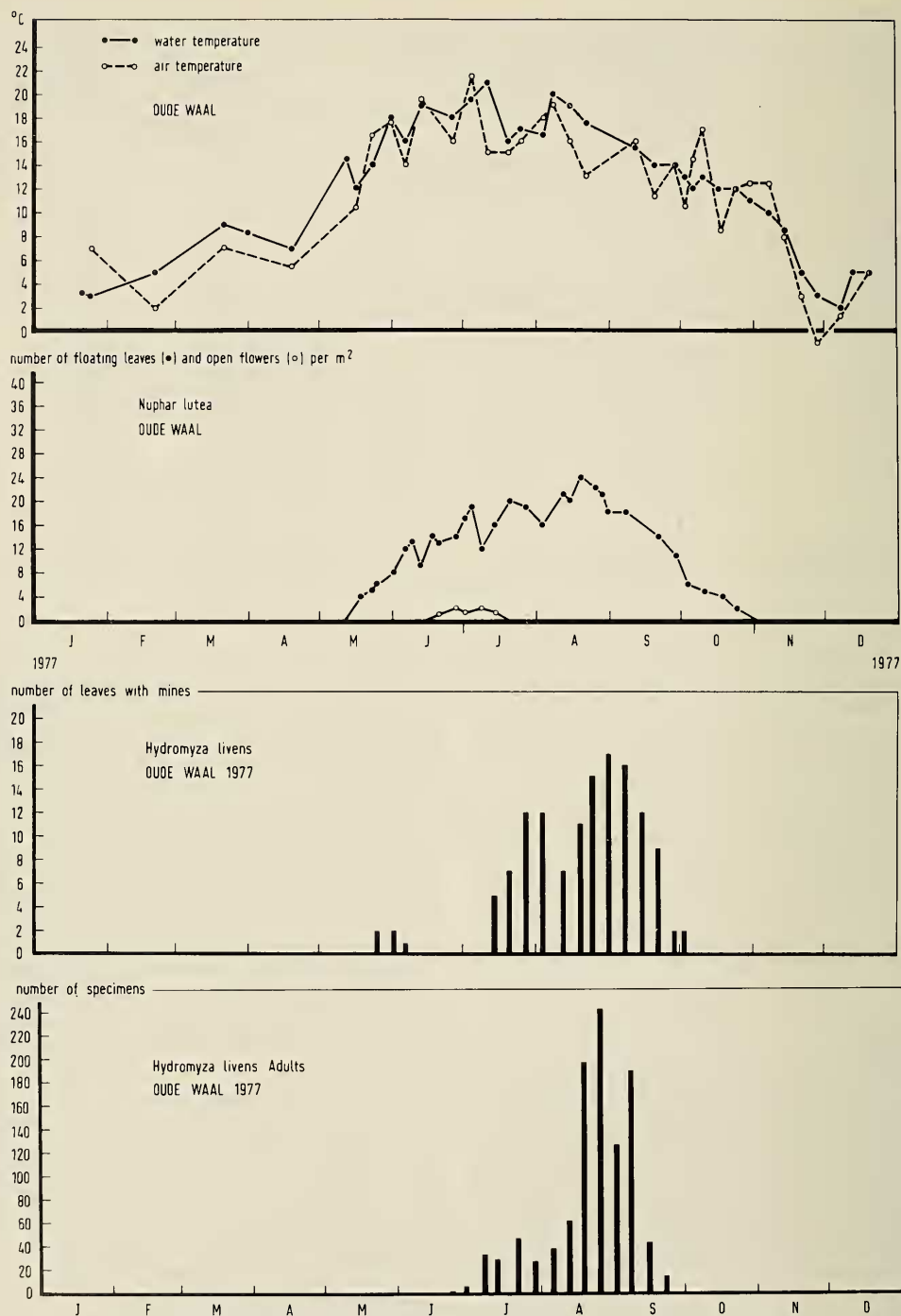
Fig. 6. Course of water and air temperature, presence of floating leaves and flowers of *Nuphar lutea* in a plot of 1 m², numbers of floating leaves affected by *Hydromyza* larvae in that plot and numbers of adult *H. livens* caught with insect-lime on the floating leaves during 1977 on the Oude Waal.
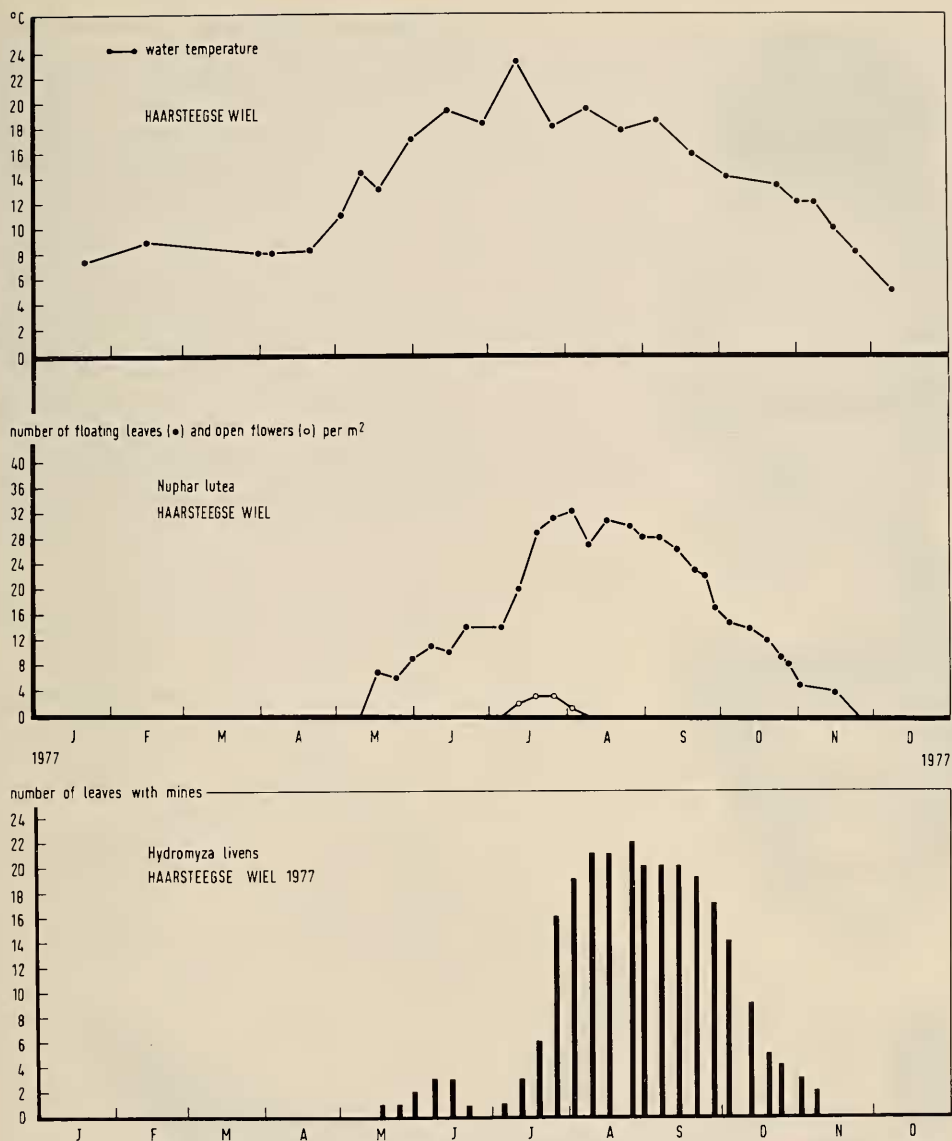
Fig. 7. Course of water temperature, presence of floating leaves and flowers of *Nuphar lutea* in a plot of 1 m² and numbers of floating leaves affected by *H. livens* in that plot during 1977 on the Haarsteegse Wiel.

generation is ca. 8 times larger than the first one.

In the Haarsteegse Wiel in 1977 both the second and third larval generations are ca. 7 times larger than the first one.

The first, and under favourable conditions also the second, generation complete their life-cycle within the growing season of *Nuphar* while the pupae of the third (under bad environmental circumstances probably also those of the second) generation hibernate and form the parents of the first generation, the next year.

That there are more generations per year is also supported by differences in behaviour and morphological characteristics of the larvae and pupae of the various generations, as will be discussed later. Schütte (1921) reported that summer and winter pupae are both present in the

beginning of August indicating that two generations overlap each other (see section on the pupa). The emergence of adults from summer pupae occurs in the same growing season of the food plant while the winter pupae hibernate. Schütte (1921) also suggested the possibility of the existence of three generations.

Adults

Morphological description

H. livens (fig. 8 and 9) is a fly of 7—9 mm length; the females (8—9 mm) are larger than the males (7—8 mm) (20 specimens of each sex were measured). The flies have a remarkably bright-yellow frons, chestnut-brown eyes and black antennae. The thorax and the abdomen are dusty blue-grey. The mesonotum has five more or less visible, grey-brown, longitudinal stripes. The legs are for the larger part red-

Fig. 8. Dorsal view of adult *H. livens* (wings omitted).

Fig. 9. Lateral view of adult *H. livens* (female).
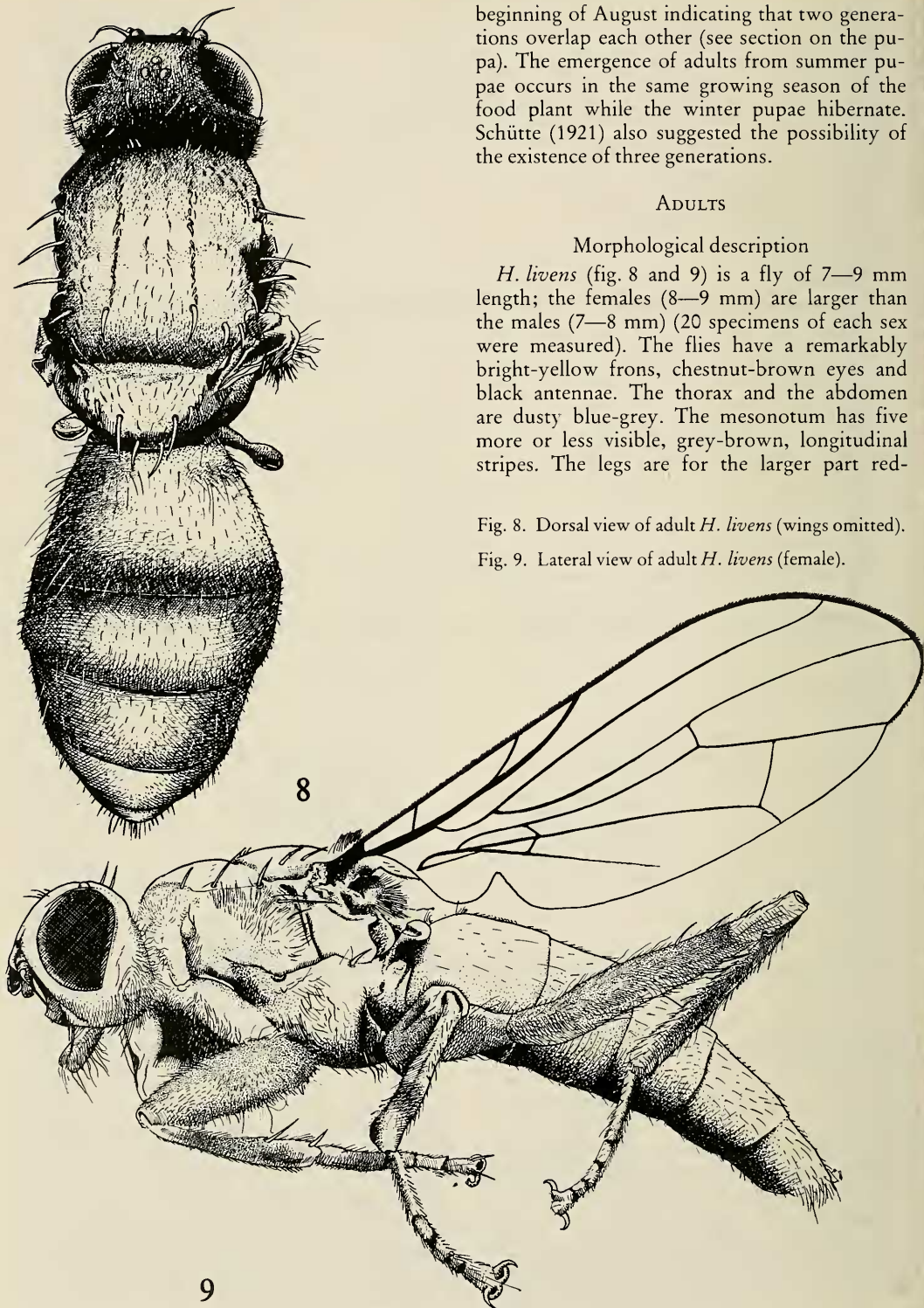
brown, with yellow-brown ginglymae; the femora are partly blackish, tinged with a dusty blue-grey. The wings are of a translucent dusty-grey while the veins are slightly brownish. Veins R 4 + 5 and M are slightly convergent towards the apex; vein 1A does not reach the margin of the wing. The relatively very short bristles on the body and the legs and the three very small proclimate frontal bristles and the single sternopleural bristle are characteristic for *Hydromyza*. For further descriptions, see Grünberg (1910), Séguy (1934), Sack (1937), Hackman (1956), and Collin (1958).

General behaviour

In the areas studied the flies usually occurred on the floating leaves of the nymphaeids *Nymphaea alba*, *Nymphaea candida*, *Nymphoides peltata*, but preferably on those of *Nuphar lutea*.

In spite of the fact that these insects have well-developed powers of flight they are not found at any great distance from the nymphaeids. They are difficult to capture and move restlessly around over the floating leaves, alternately walking or flying. They fly only short

Table 3. Temperature measurements in °C with a Wallacoy Universal Thermometer (GST 32; probes Ni-101x and Ni-106) in the flowers and on the floating leaves of *Nuphar lutea* and of the ambient water and air.

FLOATING LEAVES

Date (1977)	Tw	Ta	Tl	Tl-Tw	Tl-Ta	weather type
8-VI	16.0	18.0	19.2	3.2	1.2	sun
8-VI	16.5	18.5	19.5	3.0	1.0	sun
23-VI	—	22.6	25.4	—	2.8	sun
6-VII	24.5	28.2	29.0	4.5	0.8	sun
8-VII	23.2	24.1	25.0	1.8	0.9	bright sun
8-VII	23.4	26.1	26.5	3.1	0.4	bright sun
8-VII	23.5	25.5	25.0	1.5	−0.5	bright sun
7-VII	—	24.2	24.0	—	−0.2	heavily clouded
7-VII	—	22.0	23.0	—	1.0	clouded
29-VI	19.2	17.8	19.1	0.9	1.3	drizzle
29-VI	19.1	17.5	19.2	0.1	1.7	drizzle
29-VI	19.0	19.1	19.9	0.9	0.8	rain
29-VI	19.2	17.5	19.5	0.3	2.0	rain

FLOWERS

Date (1977)	Tw	Ta	Tf	Tf-Ta	weather type
8-VI	16.0	18.0	19.0	1.0	bright sun
23-VI	—	22.6	26.9	4.3	sun
23-VI	—	22.0	27.2	5.2	sun
6-VII	24.5	28.2	33.0	2.8	bright sun
8-VII	23.1	24.1	26.8	2.7	bright sun
8-VII	23.4	26.1	28.0	1.9	bright sun
7-VII	20.0	23.1	23.3	0.2	heavily clouded
7-VII	22.8	20.0	21.2	1.2	heavily clouded
7-VII	23.0	21.0	21.0	0.0	heavily clouded
29-VI	19.0	19.1	19.0	−0.1	drizzle
29-VI	19.2	17.5	18.6	1.1	drizzle
29-VI	17.2	17.8	19.1	1.3	drizzle
29-VI	19.1	17.5	17.4	−0.1	heavy rains

Tw = water temperature in °C measured 3 cm below water surface.
Ta = air temperature in °C measured 50 cm above water surface.
Tl = temperature upper surface floating leaf measured near midrib.
Tf = temperature of flower near stigma.

distances to reach other floating leaves or flowers in the neighbourhood; even when they are disturbed they make only short flights, seldom to open water or to the shore. Especially under sunny weather conditions the flies are very active on the floating leaves or in the flowers of *Nuphar* performing feeding, walking, flying, copulating, polishing, and sunning.

The nymphaeid floating leaves and flowers grow in maximum exposure to sunlight; consequently they can reach somewhat higher temperatures in comparison with water and air, as is illustrated in table 3 for *Nuphar lutea*. Such high temperatures probably stimulate the activity of the flies.

During bad weather conditions, e.g. heavy rain, they seek shelter under the aerial leaves of *Nymphaea alba* (leaves of this species often project entirely or partly above the water surface), in the flowers of *Nuphar*, or between the littoral helophytes, staying there more or less motionless.

Feeding behaviour

According to Eberle (1943) *H. livens* feeds in the adult stage on small insects occurring on the floating leaves of the nymphaeids, like *Hydrellia* (Ephydridae) and Chironomidae. These small Diptera are squashed by the proboscis of this predatory fly (fig. 10) and the body fluids are consumed. On the floating leaves nearly all insects which move are attacked by *H. livens*, but only small or soft skinned insects such as Nematocera are killed.

In the laboratory ten *H. livens* specimens were kept in an aquarium with *Nuphar* leaves together with some insects, which also occur abundantly on the nymphaeids, viz., the chironomid *Cricotopus sylvestris* (Fabricius) and the ephydrid flies *Hydrellia griseola* Fallén and *Notiphila brunnipes* Robineau-Desvoidy. The chironomids and the tiny *Hydrellia* were captured and consumed by *H. livens*, the larger *Notiphila* (2.8—4.5 mm) were attacked but not harmed, while dead, squashed *Notiphila*'s were consumed.

In the areas investigated adult *H. livens* was regularly observed to occur in the flowers of *Nuphar lutea*, especially in those just opened, but never in the flowers of *Nymphaea* or *Nymphoides*. The flowers of *Nuphar* possess nectaria situated on the outer side of the small petals; they produce nectar containing glucose and fructose in equal amounts as could be proved with enzymatic tests. The production of nectar

occurs especially on the first day of flowering; the flower has then a strong brandy scent (Van der Velde & Brock, 1980). The flowers of *Nuphar* also have many anthers, which produce abundant pollen. Eggs of the fly *Notiphila brunnipes* and specimens of the aphid *Rhopalosiphum nymphaeae* (L.) are usually present in the *Nuphar* flowers (Van der Velde et al., 1978; Van der Velde & Brock, 1980). Because of the regular occurrence in *Nuphar* flowers the flies were suspected of obtaining food products from them. It was however difficult in the field to observe the shy flies in the flowers without disturbing them.

In the laboratory the ten *Hydromyza* specimens were offered food in the form of *Notiphila* eggs, the aphid *Rhopalosiphum nymphaeae* and moist sugar as a substitute for nectar. The flies were repeatedly observed licking the moist sugar. In most cases this behaviour continued too long to be interpreted as a mere random inspection. Further some *Notiphila* eggs and the aphids were squashed by the proboscis of the flies and consumed. Probably adult *H. livens* feeds in the *Nuphar* flowers on nectar, *Notiphila* eggs and small insects such as aphids.

To check whether adult *H. livens* also consumes pollen, the intestines of some flies captured in *Nuphar* flowers were studied under the microscope; in the intestines diffuse material and micro-organisms could be recognized but no pollen grains.

The adult flies are numerous and it can be assumed that they play a role as pollinators of *Nuphar*. A regular flight pattern from flower to flower was never observed. However, by their regular occurrence in the flowers and by their activities, the flies certainly can cause pollination.

Spatial occurrence on the nymphaeids

Method. — To study the distribution of adult *H. livens* over the nymphaeid zone, floating leaves with insect-lime (see insect-lime method) were laid in transects from the littoral border vegetation to the open water (fig. 1).

Three *Nuphar* leaves were laid in the northern part of pond F; leaf 1 near the broad littoral border vegetation, consisting of *Typha angustifolia* L., *Rumex hydrolapathum* Huds. and *Scirpus lacustris* L., here the floating leaves of *Nuphar lutea* covered up to 60%; leaf 2, 6 m from leaf 1, in the centre of the *Nuphar* zone (maximum coverage 70%); leaf 3, 12 m from leaf 1, at the margin of the *Nuphar* zone with the open
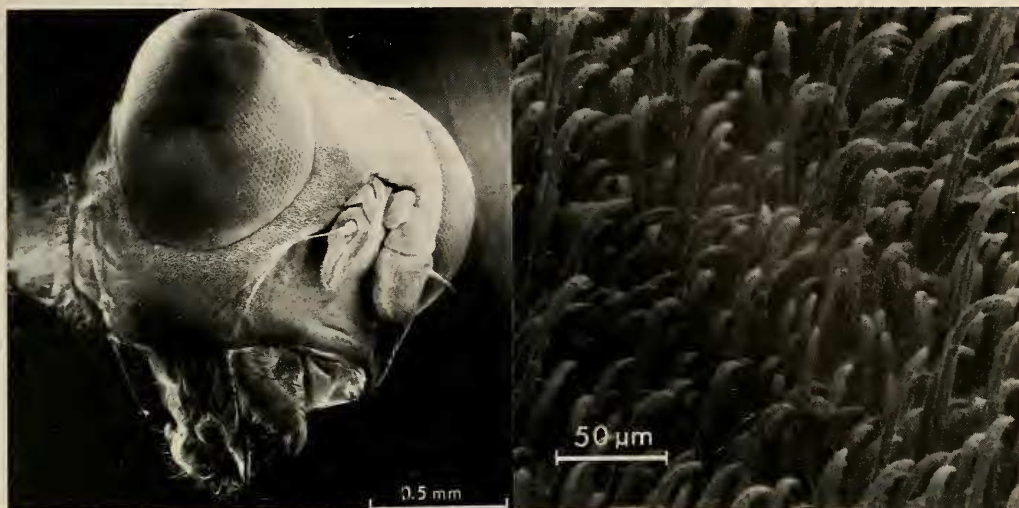
Fig. 10. Scanning electron microscope photograph of the head of *H. livens*. Note the proboscis by which small preys are squashed. Fig. 11. Scanning electron microscope photograph of hydrophobous hairs on the body of *H. livens* by which the fly avoids wetting.

water, where *Nuphar* covered up to 60% of the surface.

Two leaves were laid in a narrow *Nuphar* zone at the southern side of pond F; leaf 4 near the littoral helophyte vegetation, which borders on grassland, consisting of a narrow zone of the same plant species mentioned for the northern side, but also with *Mentha aquatica* L. (maxi-

Table 4. Absolute numbers and percentages, of adult *H. livens* and its preys caught on floating leaves with insect-lime. For the localities of the different leaves see fig. 1 and the text.

Absolute numbers per leaf and per taxon

Leaf number	1	2	3	4	5	6	total
Hydromyza livens	171	265	324	87	134	74	1,055
Nematocera spp.	359	814	2,737	734	895	599	6,138
Chironomidae spp.	227	620	2,589	663	705	463	5,267
Cricotopus spp.	83	288	1,790	437	358	142	3,098
Hydrellia spp.	346	293	137	180	154	317	1,427
	broad *Nuphar* zone			narrow *Nuphar* zone		*N. alba*	

Percentages per leaf and per taxon

Leaf number	1	2	3	4	5	6	total %
Hydromyza livens	16.2	25.1	30.7	8.2	12.7	7.0	100
Nematocera spp.	5.8	13.3	44.6	12.0	14.6	9.8	100
Chironomidae spp.	4.3	11.8	49.2	12.6	13.4	8.8	100
Cricotopus spp.	2.7	9.3	57.8	14.1	11.6	4.6	100
Hydrellia spp.	24.2	20.5	9.6	12.6	10.8	22.2	100
	broad *Nuphar* zone			narrow *Nuphar* zone		*N. alba*	

mum coverage of *Nuphar* 50%) and leaf 5 at 3 m distance from leaf 4, at the margin of the *Nuphar* zone with the open water (maximum coverage 40%).

Leaf 6, a *Nymphaea* leaf, was laid in an isolated vegetation of *Nymphaea alba*, surrounded by open water and at 6 m distance from the shore at the western side of the pond (maximum coverage of *Nymphaea* 85%).

Results. — The general distribution of the flies within the nymphaeid zone can be read from table 2, by comparing the results from the different leaves.

The flies appeared to have a distinctly higher abundance on the floating leaves bordering the open water (leaves 3 and 5); the lowest number of flies has been caught near the littoral helophyte vegetation (leaves 1 and 4).

Adult *H. livens* also showed a higher abundance on the broader *Nuphar* zone (leaves 1, 2 and 3) in comparison with the narrow one (leaves 4 and 5).

The lowest number of *H. livens* specimens was caught on the *Nymphaea* leaf (leaf 6), which is comparable with the *Nuphar* leaves 3 and 5 because of their similar location near the open water. This distribution suggests a preference for *Nuphar* leaves.

Discussion. — The higher abundance of adult *H. livens* on the nymphaeids bordering the open water may be explained by the fact that there is more food available for this predatory fly on floating leaves situated towards the open water. As mentioned before, particularly Nematocera and *Hydrellia* are food objects.

With the insect-lime method the spatial distribution of these predated insects could also be determined; the data of the most important preys are presented in table 4. When considering the spatial distribution, the absolute numbers and percentages of Nematocera and *H. livens* specimens caught on the floating leaves show the same trend. By far the largest part of Nematocera specimens is formed by the genus *Cricotopus*, mostly *C. trifasciatus* (Meigen) and *C. sylvestris* (F.). The spatial distribution of *Hydrellia* species does not show the same tendency as that of *H. livens*. The numbers of *Hydrellia* specimens on the floating leaves, however, are much smaller than those of the Nematocera (table 4).

The higher abundance of adult *H. livens* on *Nuphar* leaves in comparison with those of *Nymphaea* may be explained by the facts that the quantity of the Nematocera is relatively low on *Nymphaea* (leaf 6, table 4) and that the females of *H. livens* deposit their eggs on *Nuphar* leaves only.

Sexual behaviour and sex ratio

As already mentioned adult *H. livens* resolutely approaches all insects in motion on the floating leaves. This behaviour has the function to collect food but also to find a suitable partner. The fly can be observed regularly in copulation on the floating leaves of the nymphaeids mentioned and in the flowers of *Nuphar*.

When two *Hydromyza* specimens meet, mostly they attempt to mate, resulting in copulation in the case of two adequate partners, or in a skirmish in the case of e.g. two males. *H. livens* mostly does not show an elaborate and distinct mating behaviour. Sometimes the male, during the posturing phase of mating, toddles towards the female, while repeatedly and quickly spreading the wings sidewards. If the female accepts the invitation, she spreads the wings permitting the male to mount. It also has been observed that a male approached a female in a more aggressive way leading to copulation. During the insemination the females often continue feeding, polishing and even walking.

Males and females of *H. livens* can easily be separated from each other because they differ in size and in position of the genital aperture. The genital aperture is situated on the ventral side of the abdomen in the males and near the caudal tip of the abdomen in the females. Some samples from the insect-lime catch on the floating leaves were studied for calculating the sex ratio. The results are summarized in table 5. Usually more males than females were caught on the floating leaves; the percentage of males was 61.4. Maybe the males are more active, resulting in larger quantities of males in the catches with insect-lime. Another explanation might be a higher mortality of the females.

Deposition of eggs

As described by De Meijere (1940) and Eberle (1943), females of *H. livens* deposit eggs on the underside of the floating leaves of *Nuphar lutea*. In the study areas normally no eggs were found under the floating leaves of other nymphaeids although *Nuphar*, *Nymphaea* and *Nymphoides* locally intermingle in the same beds. Apparently the female has the ability to recognize the food plant in the presence of other nymphaeids. Only during the dry summer of 1976 eggs were found under the floating leaves

of *Nymphaea* and *Nymphoides* as well, perhaps due to the fact that the oviposition sites were strongly diminished.

Observations in the field suggest that the females inspect the floating *Nuphar* leaves before oviposition; we often observed the females walking a number of times from the leaf margin to the midrib and back again. Probably the fly in this way inspects the condition of the leaf. When a floating leaf is affected, in whatever way (even by *Hydromyza* larvae) the leaf is rejected and oviposition does not take place. From fig. 5 it can be concluded that most *Nuphar* leaves become affected by larvae of *H. livens* when the leaves have just reached the water surface. Only at the end of the season, when the numbers of adult *H. livens* are at their maximum, also older undamaged leaves (fig. 5; leaves nr. 42, 48, 81 and 65) are affected by these larvae. From these data it can be concluded that oviposition preferably takes place on just unrolled *Nuphar* leaves.

When the female has selected an adequate *Nuphar* leaf, she crawls over the leaf edge, goes into the water, and than proceeds upside down, onto the underside of the floating leaf where the egg is deposited. After approximately 20 seconds the female crawls via the leaf out of the water again and nearly immediately flies away.

Experiments in which adults were submerged showed that under such conditions the flies rise to the surface if opportunity affords, because their specific gravity is less than water. They stay under water only by clinging to a submerged object (the floating leaf). When going under water a good supply of air clings around them like a coat. The fly has a dense body-cover of small hydrophobous hairs (fig. 11). When the flies come to the surface again, they immediately lose the air coat and are apparently as dry as if they had never been under water. Because of the air coat, which they take down and the ease with which they resist wetting, oviposition can take place under water without difficulties.

A female *H. livens* deposits only one egg at a time per floating leaf. Once it was observed that a fly went down under a floating leaf on which afterwards no egg was found; when examining the underside of the leaf it appeared that a lot of periphyton occurred there, probably inhibiting oviposition.

To find out how many eggs one female of *H. livens* can deposit, a number of females were dissected and examined for eggs; 16 eggs were found at the most in the ovaries and oviducts, of which eight eggs were in a more or less mature state.

The exact way of oviposition on the underside of the floating leaves could not be observed in the field without disturbing the flies. As already reported by Eberle (1943) (and this was also observed by us in the laboratory) the females of *H. livens*, which were kept in aquaria, did not deposit their eggs under the floating leaves of *Nuphar*. Oviposition took place above the water surface on the upper side of the floating leaves and even against the glass walls of the aquaria. These eggs, which were also deposited singly, were consumed by the adults. Probably stress caused by the imprisonment changed the oviposition behaviour.

The flies in the aquaria did not survive very long, only one or two days; they easily drowned. Probably the circumstances in the aquaria (e.g. high humidity of the air) diminished their resistance in getting wet.

Eberle (1943) pointed out that the position of the deposited eggs of *H. livens* under the floating leaves of *Nuphar* gives much information about the oviposition of the females when being under water.

In the second half of August 1979, 20 more or less undamaged floating leaves of *N. lutea* were collected in the Oude Waal. The quantity of eggs per floating leaf varied from 0 to 15. Because each female only deposits one egg under a particular leaf, more females of *H. livens* must be responsible for the number of eggs per leaf. The maximum number of eggs found by us under a *Nuphar* leaf was 29. Of 100 eggs deposited by *H. livens* on the collected *Nuphar* leaves the positions were recorded by measuring the distance to the midrib and the petiole (attachment place to leaf blade). In fig. 12 the positions of these eggs are projected on a single floating leaf of *Nuphar*. The graph of fig. 13 shows the distance between these eggs and the midrib of the *Nuphar* leaf measured along the longitudinal axis of the eggs.

According to these data and those of Schütte (1921) and Eberle (1943) several regularities in the positions of the eggs appeared to exist, viz.:

(a) The broad rostral end of the egg is situated mostly towards the midrib. In dissected females the more pointed caudal end of the egg lies more towards the oviduct, during oviposition this end leaves the abdomen before the broader end. During oviposition, therefore, the female must be directed with her head towards the midrib.
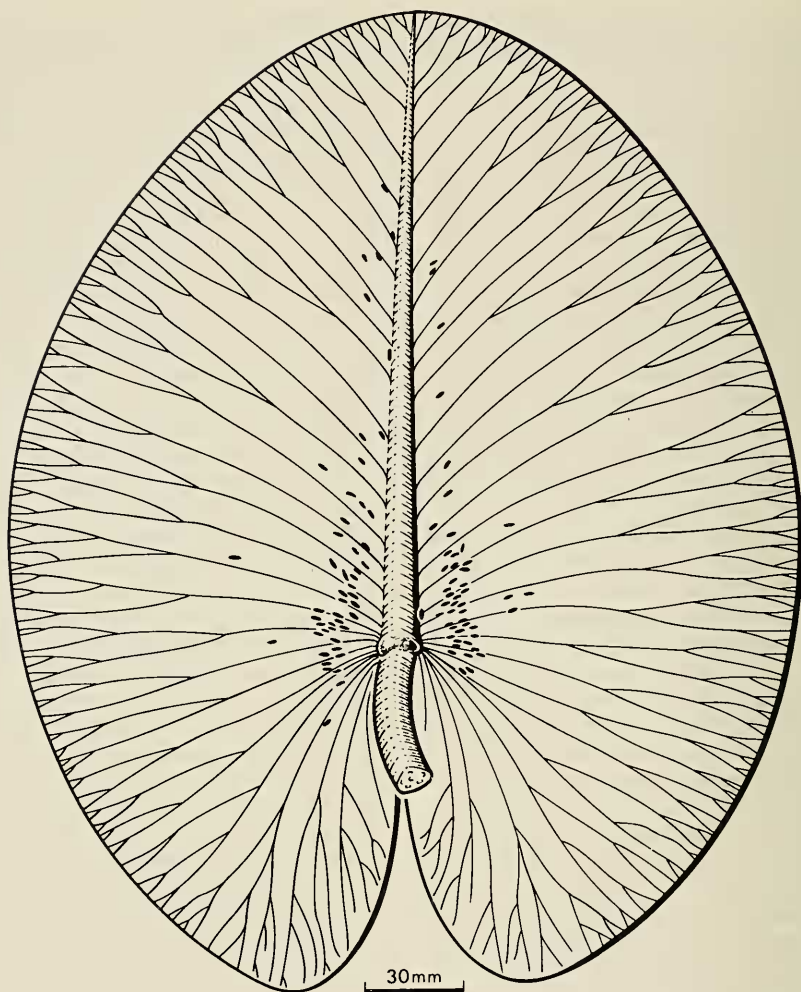
Fig. 12. The positions of 100 eggs of *H. livens* (collected from 20 leaves) projected on the underside of a single *Nuphar* leaf.

(b) The longitudinal axis of the egg is mostly situated parallel to the lateral leaf nerves, mostly between two of them.

(c) Most of the deposited eggs can be found near the basis of the midrib.

(d) Most of the eggs are deposited approximately 7—10 mm from the midrib (fig. 13).

From these data it can be concluded that a female of *H. livens* mostly crawls into the water via the edge of the broadest part of the floating leaf where the lateral nerves are dichotomously branched. When under water, clinging upside down to the leaf and covered with an air coat, the female crawls towards the midrib, guided by a lateral leaf nerve, which is translucent. Probably the visual observation or touching of the midrib is a strong stimulus for oviposition because the distances between the eggs and the midribs mostly were approximately the length of the flies. These conclusions agree with those of Eberle (1943).

Spatial occurrence of egg deposition

In order to find out where egg deposition mostly takes place within the nymphaeid zone, both in the Oude Waal and Haarsteegse Wiel, in 1977 regularly 15 floating *Nuphar* leaves were collected at random at three sites, viz., 15 near

the littoral border vegetation, 15 in the middle of the *Nuphar* zone and 15 near the open water. Leaves were collected every month from May until September in the Oude Waal and every two weeks from June until September in the Haarsteegse Wiel. The eggs and larvae occurring under and in the leaves were counted per site per date.

In the Oude Waal in total 62 larvae and eggs were counted on the leaves bordering the littoral helophyte vegetation, 38 on leaves from the middle of the *Nuphar* zone and 65 on floating leaves from the location near the open water.

In the Haarsteegse Wiel, in total 81 larvae and eggs were found on the leaves near the littoral border vegetation, 79 on leaves from the middle of the *Nuphar* zone and 94 on leaves bordering the open water.

It can be concluded that oviposition in the Oude Waal takes place more often under leaves at the two edges of the *Nuphar* belt than under leaves in the middle of the *Nuphar* zone. The results from the Haarsteegse Wiel show this trend less clearly.

From the data obtained with the insect-lime method it appeared that the adults were definitely more abundant on the nymphaeids bordering the open water because of the higher abundance of food organisms there. The large number of eggs and larvae under and in floating leaves of the sites near the open water can be explained in this way. The high frequency of egg deposition under floating leaves bordering the littoral helophytes may be explained by the fact that wind and wave action are less pronounced here.
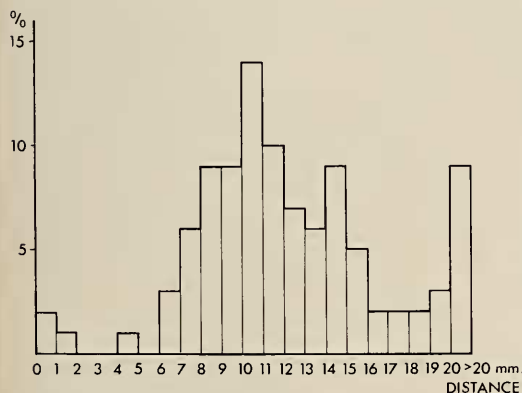

Fig. 13. The distances of 100 eggs of *H. livens* to the midribs of the floating leaves on which they were deposited, measured along the longitudinal axis of the eggs (see also fig. 12).

Mortality and predation

As may be concluded from fig. 6, the numbers of adult *H. livens* decrease at the end of the growing season of *Nuphar*. The mortality of adults may have several reasons, e.g. falling temperatures, diminishing of the floating leaf area (figs. 5, 6 and 7) and lack of food (table 2). Exhaustion of females and risks under water during oviposition, such as predation by fish, might also cause mortality; the sex ratio data mostly showed a majority of males (table 5). After heavy rain the population size of adult *H. livens* seems to be diminished. Although the flies have hydrophobous hairs, they easily drown when their skins become wet. Probably a long-lasting contact with water or even very humid conditions (aquaria) diminish their resistance against getting wet. Predation on adult *H. livens* has never been observed by us. However, Odonata, swifts (*Apus apus* (L.)), swallows (*Hirundo rustica* L., *Delichon urbica* (L.)), terns (*Sterna hirundo* L., *Chlidonias niger* (L.)) and the Green frog (*Rana esculenta* (L.)) prey on the insects from the floating leaves and thus can occasionally catch *H. livens*.

THE EGG

Morphological description

The eggs of *H. livens* have a length of 1.9—2.0 mm and a width of 0.5—0.6 mm. Freshly laid eggs are yellow-white in colour, a few hours before hatching they become darker. The eggs have the appearance of a boat (fig. 14a), with differently shaped ends: the caudal end is bluntly pointed, while the broader rostral end is more rounded and contains the micropyle. A straight, acute carina extends longitudinally from end to end and runs medially along the bottom of a rather deep, broad, longitudinal fossa (fig. 14b), dividing it into two similar parts. This divided fossa is laterally bordered by two other longitudinal carinae, which run almost parallel to the median carina, converging and uniting with the ends of the egg. The eggs are always deposited singly under the floating leaves of *Nuphar* and are firmly fixed to the substrate so that it is nearly impossible to separate them from a floating leaf without damage to the chorion or the leaf tissue. Apparently a small amount of sealing fluid accompanies the egg at oviposition causing the firm attachment to the floating leaf.

Eggs have been studied by means of scanning

Table 5. Sex distribution and the percentage of males in samples of *H. livens* caught with insect-lime.

Date (1977)	Number of specimens examined	Males	Females	percentage of males
30-VI	2	1	1	50.0
12-VII	13	11	2	84.6
21-VII	19	12	7	63.2
28-VII	7	3	4	42.9
5-VIII	25	13	12	52.0
12-VIII	24	6	18	25.0
25-VIII	125	82	43	65.6
1-IX	91	63	28	69.2
8-IX	5	0	5	0
Total	311	191	120	61.4

electron microscopy; in this way the external and internal appearance of the chorion could be studied (fig. 14). The external surface of the chorion, especially near the carinae, appears more or less reticulate, being composed of polygonal units (fig. 14b). The reticulation is elongated in the direction of the long axis of the egg and within the netlike structures many pores can be recognized (fig. 14b and 14c).

To study the internal structure of the chorion the eggs were sliced with a razorblade and examined with the scanning electron microscope (fig. 14d, e and f). The chorion appeared to possess cavities, which are apparently in contact with the pores in the external walls. The chorion is distinctly thicker at the carinae and the depression between them than on the lateral sides, as shown in fig. 14d.

The function of the chorion

The chorion protects the eggs against certain predators but also can function as a plastron. According to Hinton (1967, 1971) the terrestrial eggs of the majority of insects have structures in the chorion which have the function to hold air to maintain respiration on becoming wet, e.g. by a rain shower; the chorion of many aquatic and semi-aquatic eggs is solid.

It appears from the scanning electron micrographs (fig. 14) that the chorion of the aquatic egg of *H. livens* contains cavities. These cavities possibly hold an air layer which functions as a plastron. Hinton (1960) has shown that a system of hydrofuge structures in the chorion can form the architecture for a permanent, unshrinkable, physical gill, a plastron. An egg with a plastron can remain immersed indefinitely and obtains the oxygen it requires from the ambient water, provided that the water is well-aerated.

Normally the eggs of *H. livens* are deposited under the floating leaves of *Nuphar* so during their development into larvae they are immersed in the extreme upper layer of water. In natural habitats, such as the Oude Waal, the water under the floating leaves is well-aerated. On 25 August 1977 the amount of oxygen in the water of the Oude Waal was measured with an oxygen meter (Y.S.I. model 151A). Directly under the floating *Nuphar* leaves the measured oxygen saturation percentage was 78%. At depths of 50, 100 and 150 cm (near the bottom) the oxygen saturation percentages diminished and were 75, 70 and 45% respectively.

Eggs with a plastron are able to survive under the floating leaves because of the well-aerated conditions.

In the laboratory, eggs of *H. livens* normally developed into larvae when floating leaves with eggs were kept floating in aquaria and also, when they were kept under very humid conditions outside the water. The eggs, however, soon desiccated when floating leaves with eggs were kept in a dry environment outside the water. Also when floating leaves with eggs were kept on the bottom of an aquarium, 20 cm below the water surface in non-aerated water, the eggs had not yet hatched when the leaves had already decayed; probably the eggs did not develop because of depletion of oxygen. It can be concluded that the eggs develop in well-aerated water or in very humid air; the chorion, however, is not adapted to prevent desiccation and probably forms the architecture for a physical gill or plastron.
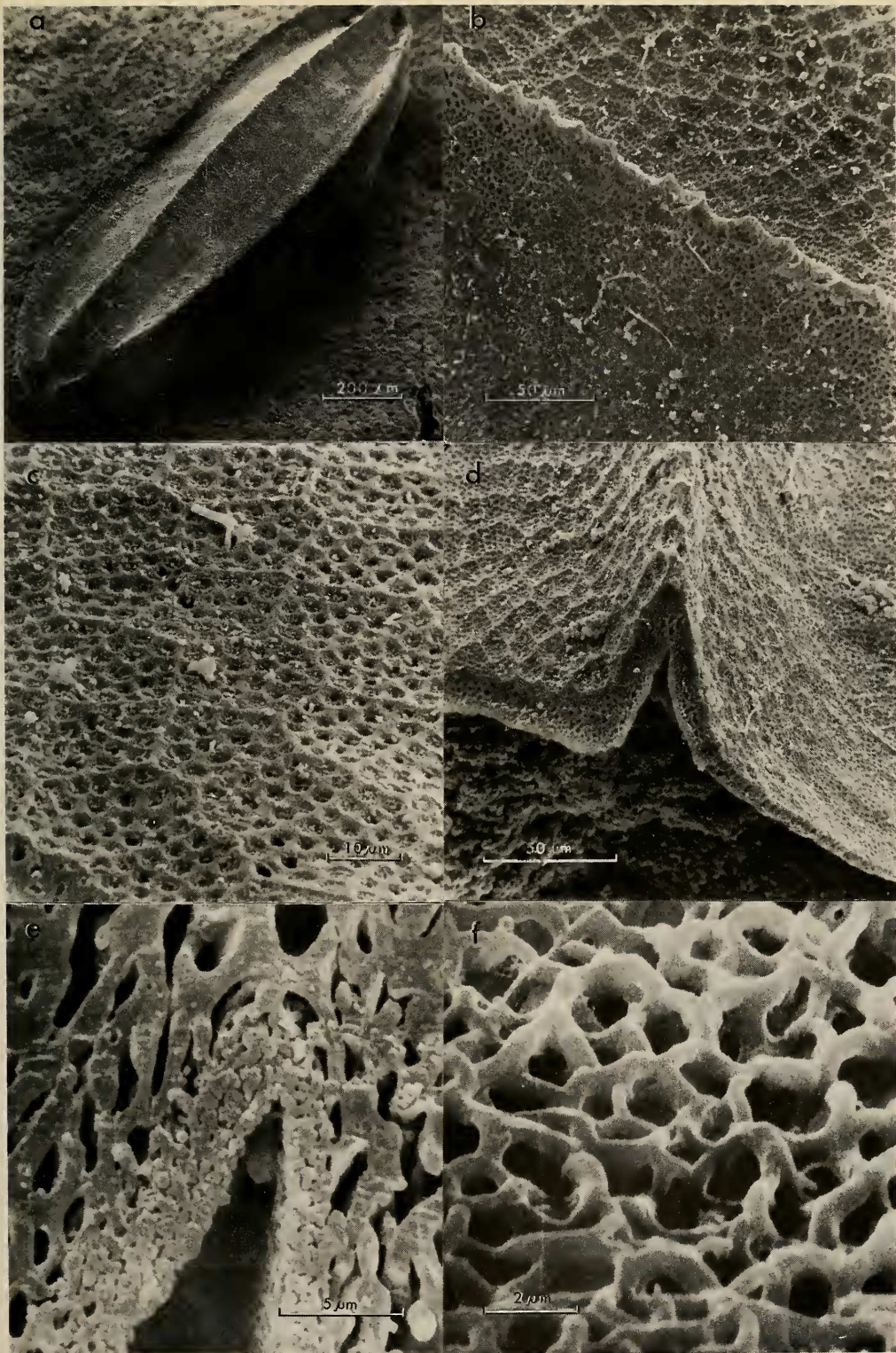
Fig. 14. Scanning electron microscope photographs of the egg stage of *H. livens*: (a) overall view, note the micropyle at the frontal end; (b) detail of the chorion near the median carina; (c) detail of the chorion showing polygonal units and pores; (d) transversal section, showing the internal structure of the chorion near a carina; (e) detail of the internal structure of the chorion, showing many pores and cavities; (f) detail of the innerside of the chorion also showing pores.
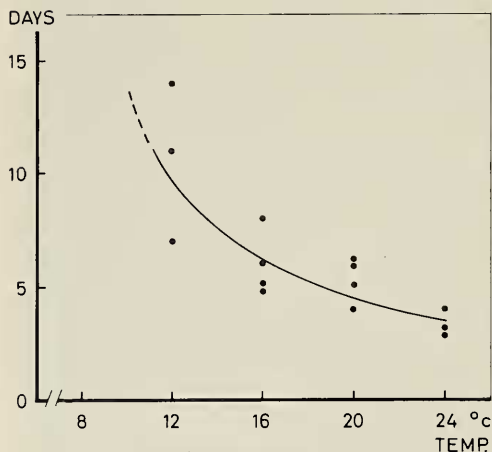
Fig. 15. Duration of the development of *H. livens* eggs into larvae in relation with temperature.

Fig. 16. Photograph of a *H. livens* larva sampled from a leaf blade.

Development in relation to temperature

Eberle (1943) already discussed the fact that the development of eggs into larvae is dependent on temperature. In spring, when the water is relatively cold, the duration of the development can last out up to two weeks, while in summer, when the water is warmer, the larvae hatch after 3 to 4 days after the time of egg deposition (Eberle, 1943).

It is difficult to study the development of the eggs in relation to temperature under controlled circumstances because it is difficult to obtain enough eggs of the same age which are freshly deposited by the females of *H. livens*. As already discussed one can only sporadically observe the oviposition in natural habitats, while the flies in captivity do not deposit their eggs in the normal way under the floating leaves. In order to obtain eggs which were more or less of the same age, 25 undamaged, young leaves of *Nuphar*, under which no eggs were deposited, were marked in the Oude Waal at the end of August 1979. After 24 hours these leaves were collected and 19 eggs of *H. livens* were obtained from them. The differences in age of these eggs could be 24 hours at most; the temperature of the Oude Waal water was at that time 18 °C. In the laboratory the floating leaves with eggs were kept in aquaria and placed in different climate chambers which had constant temperatures of 8, 12, 16, 20 and 24 °C. Temperatures within this range had also been measured in the Oude Waal (fig. 6). In the climate chamber of 8 °C three eggs were placed, in the other cham-
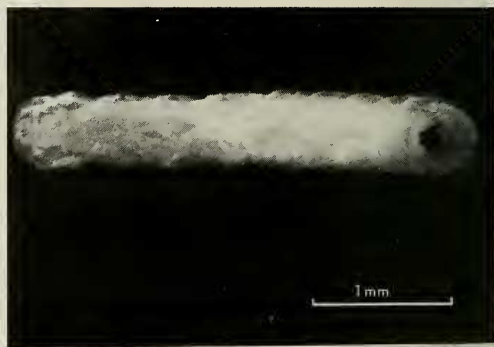
bers four each. By daily observations the development of the eggs into larvae was followed (see fig. 15).

The data thus obtained confirm that the development of the eggs is indeed dependent on temperature and that the development goes faster at temperatures which are normally measured in summer in comparison with colder circumstances in spring and autumn. Below a certain temperature, between 8 and 12 °C, the eggs do not develop at all into larvae. The large differences in developmental rate of the eggs, especially in the climate chambers of 12 °C and 16 °C, are probably caused by the way the eggs were obtained, viz. at a temperature of 18 °C.

THE LARVA

Morphological description

The larva of *H. livens* (fig. 16) is yellowwhite in colour with the exception of the black cephalopharynx skeleton (fig. 18), the brown, kidney-shaped, frontal stigmata and the dark terminal stigmata (fig. 17).

The anterior stigmata consist of short processes, each with several buds; the total number of buds on one stigma being about 200 (De Meijere, 1895). According to Schütte (1921) there is no difference between the number of stigmatic buds of larvae and pupae of the different generations. In the summer larvae (in our case the first and second generation) the diameters of these buds are smaller, however, than in the winter larvae (in our case the third generation). The anterior stigmata are not yet visible on freshly hatched larvae.

In the translucent body the long, green intestine, the main tracheae and the very well devel-

Fig. 17. Terminal stigmata (spiracular disc) of a *H. livens* larva. Fig. 18. Cephalopharynx skeleton of a larva of *H. livens*.

oped salivary glands are visible. The digestion tract of the full-grown larva is at most 8.5 cm long (about eight times the total length of the larva) (Schütte, 1921).

The body is cylindrical and elongate, and consists of 12 more or less visible segments. Some intersegmental grooves are very distinct. The anterior end of the body is moderately rounded with the exception of the acute, emergent teeth of the cephalopharynx skeleton. Posteriorly, the body is bluntly tapering to the more or less rounded or acute chitinous projections of the terminal stigmata (fig. 17).

The integument is covered with pointed, chitinous projections which are directed backwards. These projections are rather uniform in size and shape over the body except on the anterior margin of the first thoracic segment, where they are larger and more distinct. On the younger larvae, bristle-like projections can be recognized above the mouth-hooks. In fig. 19, scanning electron microscope photographs of heads of larvae of *H. livens* are presented. The larva of fig. 19a was collected from a floating leaf of *Nuphar lutea* and was 2—3 days of age. The larva of fig. 19b was collected from a petiole of a floating *Nuphar* leaf and is a few days older.

According to Schütte (1921) the larvae of the summer generation measure 9.5 mm in length at a width of 2.5 mm, while the length and width of larvae of the last generation measure 11 and 3
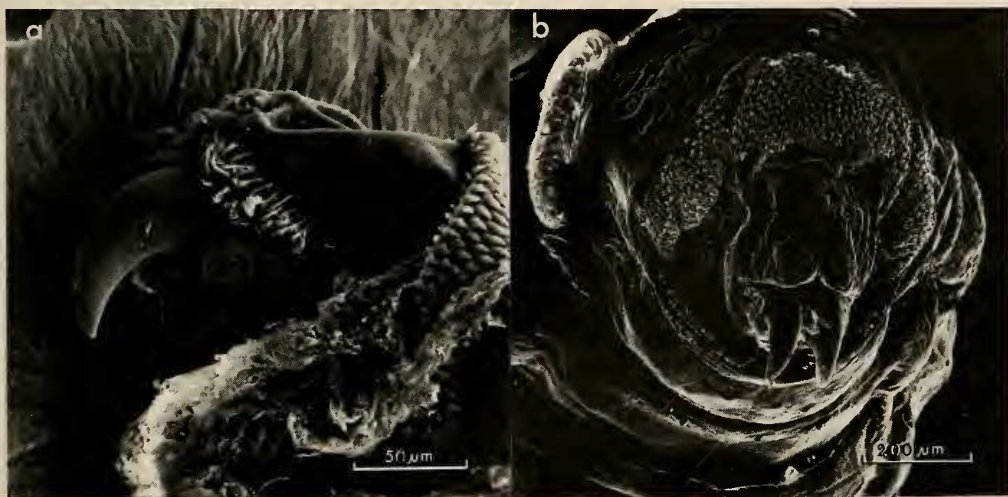

Fig. 19. Scanning electron microscope photographs of the heads of two *H. livens* larvae, sampled from a leaf blade (a) and from a petiole (b).

mm, respectively. According to Eberle (1943) full-grown larvae of the first generation measure 9 mm in length, while the mature larvae of the last generation can reach a length of 11 mm.

In the Oude Waal full-grown larvae of the last generation were 10.5—13.0 mm in length, with a width of 1.5—2.5 mm.
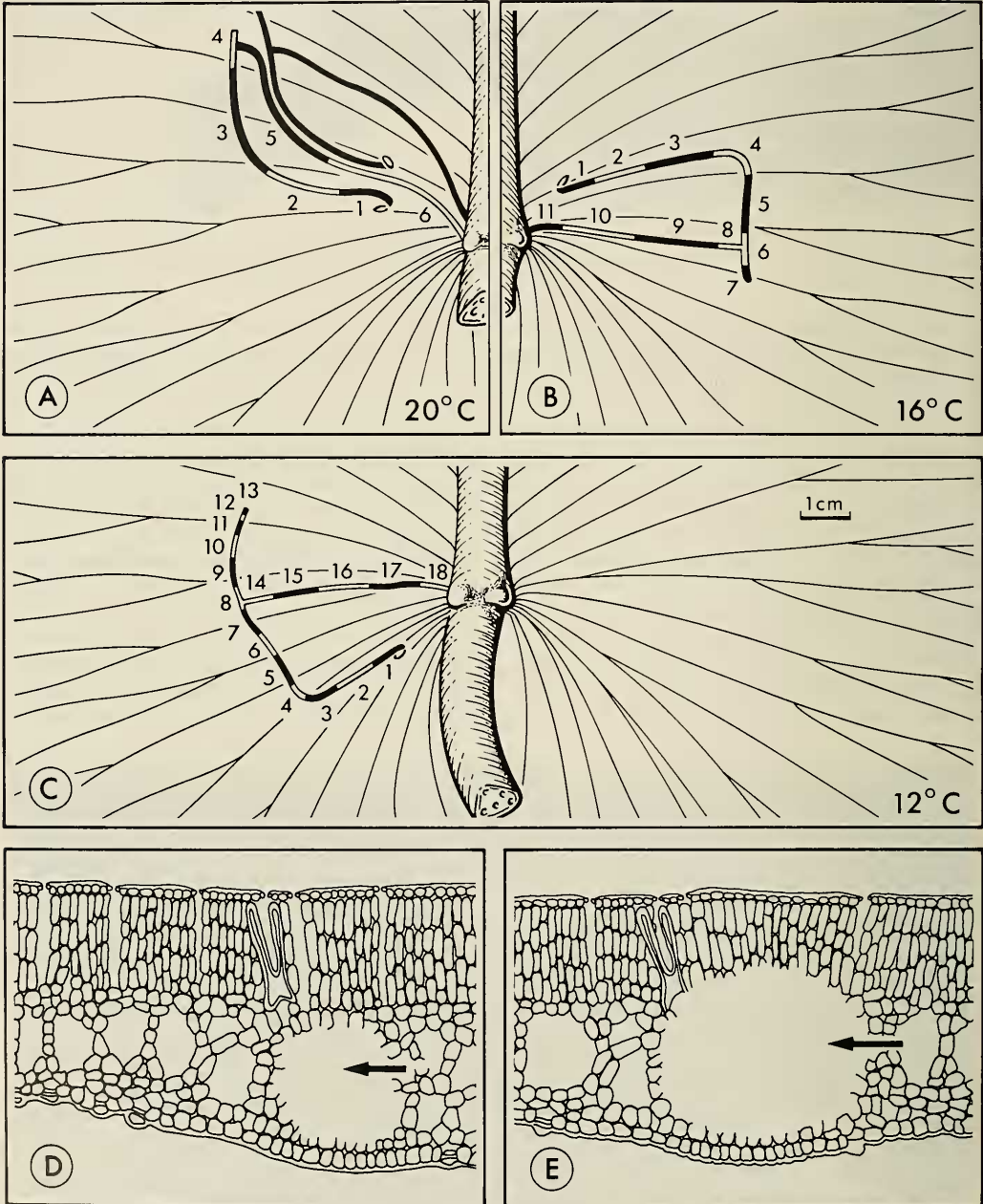
According to Schütte (1921) there are four

Fig. 20. Daily length increase of mine tracks of three *H. livens* larvae in *Nuphar* leaves at a temperature of 20 °C (A), 16 °C (B) and 12 °C (C), respectively. Each number corresponds with a day. Transversal section of a part of a *Nuphar* leaf with a mine track (arrow) of a just hatched larva (D) and an older larva (E) in the leaf blade.

Fig. 21. Photograph of a part of a *Nuphar* leaf with mine tracks of *H. livens* larvae.

instars; this author also gives an extensive anatomical description of the larva and its way of nutrition.

The process of hatching from the egg

Shortly before the time of hatching, the egg becomes darker in colour, indicating that the larva within the egg is fully developed. The place of emergence of the larva through the egg shell is very constant. With the aid of relatively large, acute, chitinous mouthparts the larva makes an exit through the egg shell on the side next to the leaf. The position of the exit hole is determined by the position of the larva in the egg. So the exit is made near the blunt, broad, rostral end of the egg, which is mostly directed towards the midrib of the floating leaf. Via this hole the larva bores directly through the lower epidermis into the mesophyll of the floating *Nuphar* leaf. After the process of hatching the empty egg shell remains sticking to the leaf, closing off the exit, so that water is not able to enter the mine gallery in the leaf.

General feeding behaviour

In the investigated areas the larvae of *H. livens* feed on the floating leaf and petiole tissue of *Nuphar lutea*. During the early period of feeding only the spongy parenchyma of the floating leaf is consumed, while in a later stage, when the larva has increased in volume, also the palissade parenchyma of the mesophyll is eaten (fig. 20d and 20e).

While eating through the floating *Nuphar* leaf the larva produces a mine gallery in it, and afterwards also in the petiole where the larva eats itself spirally downwards (fig. 21 and fig. 22c).

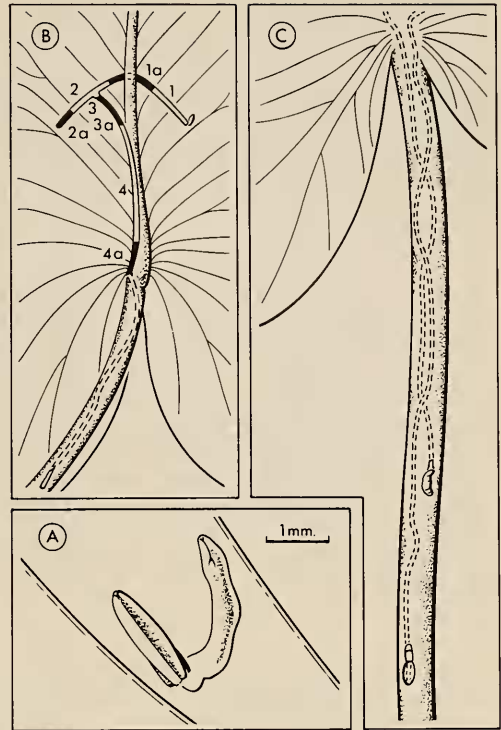With the aid of the large acute mouth-hooks

Fig. 22. (A) Just hatched larva of *H. livens* in its mine track and the empty egg shell. (B) Larval consumption by day (white) and by night (black and marked with a) in a *Nuphar* leaf. (C) Mine tracks of *H. livens* in a petiole of a *Nuphar* leaf. (Modified after Eberle, 1943.)

the larva loosens the plant cells while making mowing movements with the head. According to Schütte (1921) the larvae of *H. livens* secrete digestion enzymes which dissolve the plant cells before they are ingested. Consequently one can find no recognizable fragments in the intestines of the larvae.

In the floating leaves and petioles of *Nuphar* many sharp, hair-like branched trichosclereids occur which consist of calcium oxalate. The secreted digestion enzymes also dissolve these sharp trichosclereids; the intestines of the larvae are not harmed by them in this way. The calcium oxalate is transformed into calcium carbonate in the Malpighian organs (Schütte, 1921).

Eberle (1943) already demonstrated that the larva of *H. livens* feeds by day and by night, as is illustrated in fig. 22b. The larval consumption and consequently the length of the mine is somewhat larger by day than by night, probably due to differences in temperature between day and night.

Regularities in larval feeding and mine patterns

According to Schütte (1921) the larvae are negatively phototactic, which may help and guide their position in the leaf tissue. According to Eberle (1943) and to our own observations the way of larval feeding shows regularities, viz.:

(a) The larva, which has recently left the egg, mostly creates a mine gallery that makes a sharp bend of approximately 180° (fig. 22a).

(b) After that the larva mostly mines in the direction of the leaf margin, more or less parallel to the lateral leaf nerves. When eating towards the leaf edge, the thickness of the mesophyll decreases while the volume of the larva in-
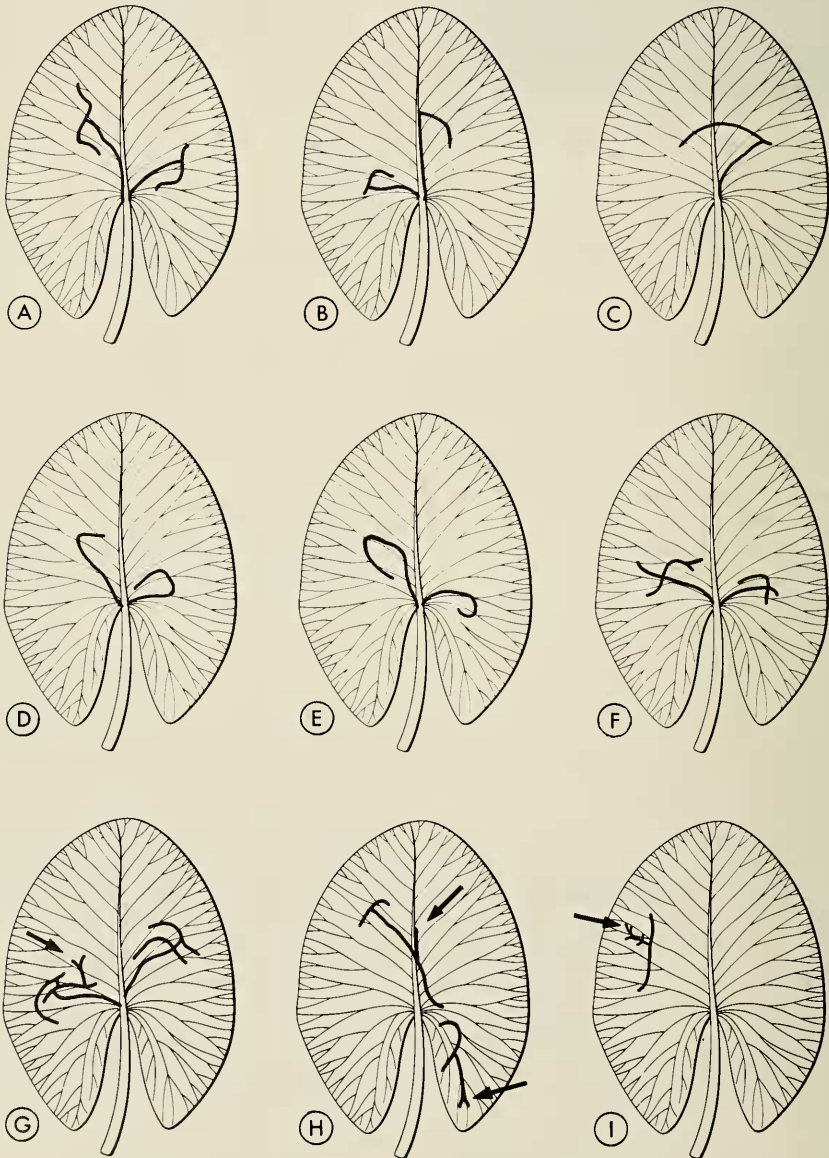

Fig. 23. Various types of mine tracks of larvae of *H. livens* in leaves of *Nuphar lutea*. The arrows show the locations of dead larvae.

creases; this results in a more or less sharp gradual bend of the mine gallery parallel to the leaf margin (fig. 23a—e).

(c) After this the feeding behaviour of the larva suddenly changes. This change is correlated with the first moulting period of the larva. After having cast the old skin, the larva mines more or less at right angles to the previously created part of the mine gallery in the direction of the midrib or petiole of the floating leaf (fig. 23a—e).

(d) On reaching the petiole the larva mines spirally downwards where ultimately the full grown larva pupates.

These regularities in larval feeding behaviour cause regularities in the shape of the mine galleries and consequently one can distinguish certain mine types, in the leaf blades, viz.:

(1) The T-shaped mine gallery (fig. 23a, b and c). This type is created by larvae which after the first moulting period crawl backwards in the older part of the mine gallery before starting to eat in the direction of the midrib or petiole.

(2) The arch-like mine gallery (fig. 23d and e). In this type, the larva does not crawl backwards after moulting.

(3) The cross-like or irregularly shaped mine gallery (fig. 23f, g, h, i). This type of mine gallery is the result of disturbances in the mining behaviour of the larva, or it is caused by the damaged state of the leaf blade. Although the eggs of *H. livens* are mostly deposited under young and undamaged floating leaves, these leaves might be damaged before the eggs have hatched. This damage on the leaves of *Nuphar lutea* might, for instance, be caused by the feeding by the Coot (*Fulica atra* L.), the gastropod *Lymnaea stagnalis* (L.), the beetles *Donacia crassipes* F. and *Pyrrhalta nymphaeae* (L.), the caterpillar *Nymphula nymphaeata* (L.), but above all by other *H. livens* larvae. When the floating leaf is not damaged too much, the younger larva has the ability to avoid the older affected leaf part (fig. 20a).

When the larval numbers are at their maximum, there is a great chance that a larva of *H. livens* crosses an older mine gallery. In that case the larva sometimes crosses the mine under a right angle but mostly the larva makes use of the older gallery for a while (fig. 23g). This can result in creeping into wrong directions of the larva, and, consequently, in an irregular shape of the mine gallery. It also happens that a larva mines in the wrong direction after the first moulting (fig. 23h, i) also resulting in an irregu-

lar shape of the mine gallery in the leaf blade.

In order to get an idea of the occurrence of the different types of mine galleries, 34 floating leaves were collected in the Oude Waal on 11 September 1979. In total, 207 mine galleries could be recognized in these leaves. Of the mines 60.5% could be classified within the T-shaped type, 30.5% in the arch-like type, and 9.0% in the cross-like or irregular shaped type.

Feeding behaviour and temperature

In the laboratory the larval consumption in floating leaf blades was followed in different climate chambers.

In fig. 22b the larva has reached the petiole on the 4th day. This also happened with a larva in the laboratory in the climate chamber of 24 °C. In the climate chamber of 20 °C a larva reached the petiole on the 6th day, while at constant temperatures of 16 °C and 12 °C this happened on the 11th an 18th day after the moment of hatching from the egg, respectively. The daily consumption of the three larvae in the climate chambers of 20 °C, 16 °C and 12 °C was followed in detail (fig. 20 and table 6).

Although the consuming activity of only a few larvae was followed under controlled cir-

Table 6. Daily length increase of mine tracks in mm of three *H. livens* larvae in leaf blades of *Nuphar* at temperatures of 20, 16 and 12 °C, respectively.

Number of days	20 °C mm	16 °C mm	12 °C mm
1	12	8	7
2	16	10	8
3	23	11	7
4	8	9	6
5	32	13	7
6	34	7	6
7	—	2	7
8	—	5	4
9	—	17	5
10	—	15	6
11	—	7	4
12	—	—	1
13	—	—	1
14	—	—	5
15	—	—	8
16	—	—	11
17	—	—	10
18	—	—	5
Total length of mine track	125	104	108 mm
Mean length per day	20.8	9.5	6.0 mm

cumstances one can draw some general conclu-
sions from the data thus obtained. The con-
suming activity is temperature dependent and
apparently the development rate is faster under
warmer conditions during the summer, than in
spring and autumn when colder air and water
temperatures occur.

The daily consumption of the larvae is not
constant at a constant temperature. Generally
the larvae consume more when they become
older, only during the moulting period the lar-
val consumption is very low (fig. 20, table 6).

Also the time needed for moulting seems to
be temperature dependent and consequently
takes a longer time under colder circumstances.

Differences in consumption and feeding behaviour between the generations

According to Schütte (1921) and Hendel
(1928) the length of the mine galleries in the

petioles of the summer and winter pupae is ca.
10 cm and 20—25 cm respectively. In order to
get an impression of the larval consumption of
plant tissue of the various generations both in
the second half of July and in September, 1977,
a number of floating leaves and leaf stalks of
Nuphar were gathered in the Oude Waal. The
lengths of 25 mine tracks in the leaf blades and
another 25 in the leaf stalks were measured (ta-
ble 7).

The measurements of July, 1977, correspond
with the second generation of *H. livens*. This
generation, as well as the first one, completes its
life cycle within one growing season of *Nuphar*.
The lengths of the mine galleries measured in
September correspond with the third genera-
tion, which generation hibernates as pupa.

Three stages of the mine track have been dis-
tinguished in the floating leaf and petiole, viz.:
    (1) mine stage 1; this stage corresponds with

Table 7. Lengths of 25 mine tracks of *H. livens* larvae in leaf blades and petioles of *Nuphar*, in July and September, 1977. For explanation of the mine stages, see the text.

July, 1977

n	Mine stage 1 in mm	Mine stage 2 in mm	Total length in leaf blade (mm)	Mine stage 3 in petiole (mm)
1	37	27	64	37
2	34	84	118	36
3	25	76	101	29
4	33	33	66	48
5	34	35	69	38
6	24	36	60	32
7	52	51	103	29
8	38	59	97	39
9	31	36	67	38
10	30	116	146	29
11	39	104	143	54
12	53	65	118	40
13	38	48	86	30
14	41	55	96	84
15	40	63	103	58
16	54	79	133	41
17	41	50	91	40
18	48	35	83	42
19	57	68	125	71
20	60	207	267	49
21	49	61	110	41
22	62	75	137	44
23	40	55	95	43
24	41	56	97	35
25	38	39	77	39
mean length	41.6	64.5	106.1	42.6
SD	± 10.3	± 36.9	± 41.8	± 12.9

the consumed length of the mine gallery before the first larval moulting period in the leaf blade;

(2) mine stage 2; this stage corresponds with the consumed length of the mine gallery in the leaf blade after the moulting of the larva;

(3) mine stage 3; the length of the mine gallery in the petiole.

The results of the measurements are summarized in table 7. The differences in the mean length of the mine galleries in the leaf blade between the second and the third larval generation of *H. livens* are not large. The differences in mean length of the mine galleries in the petioles, however, are very conspicuous between these generations with mean lengths of 42.6 ± 12.9 and 95.1 ± 28.3 mm, respectively. Therefore, the total length of the mine and consequently the consumption of plant tissue of the generation that completes its life cycle within the growing season of *Nuphar* is smaller than that of the one which hibernates as pupa during the next winter. Apparently the generation that hibernates needs more energy to survive this cold period.

Also the feeding behaviour of the first and second generation differs from the third one, in the Oude Waal. Schütte (1921) and Eberle (1943) already recorded that the fullgrown larvae of the first generation construct a provision for the emergence of the adults in the form of a window. In constructing this window the fullgrown larva eats towards the exterior of the petiole until it reaches the epidermis. Here it removes all surrounding tissue from a more or less circular area with a diameter of 2—3 mm, which is destined to be the window and is composed of the epidermis only. The window is only large enough to allow the passage of the emergent adult. In the Oude Waal the fullgrown larvae of both the first and second generation construct such a provision.

According to Eberle (1943) and according to our own observations the fullgrown larvae of the last generation (in our case the third one) do

(Continuation from page 84)

September, 1977

n	Mine stage 1 in mm	Mine stage 2 in mm	Total length in leaf blade (mm)	Mine stage 3 in petiole (mm)
1	50	64	114	90
2	59	78	137	88
3	41	90	131	75
4	42	55	97	80
5	41	62	103	73
6	55	75	130	93
7	37	42	79	101
8	35	120	155	80
9	48	61	109	80
10	42	50	92	86
11	51	66	117	102
12	40	155	195	94
13	45	52	97	76
14	57	55	112	90
15	50	77	127	78
16	51	60	111	72
17	47	71	118	116
18	59	82	141	75
19	35	121	156	124
20	60	75	135	74
21	34	41	75	80
22	46	35	81	88
23	39	74	113	197
24	35	61	96	150
25	47	73	120	116
mean length	45.8	71.8	117.6	95.1
SD	± 8.1	± 26.9	± 27.0	± 28.3

not construct windows for emergence. When they have pupated they stay as long as possible in the petioles, in the broadened end part of the mine gallery.

Mortality

Predators of the larvae of *H. livens* were never observed. The floating leaves and petioles of *Nuphar* not only provide the larvae with food and oxygen, but also with protection against possible predators.

As already discussed a damaged state of the floating leaf can cause irregularities in the mining behaviour of the larvae, resulting in their death (fig. 23g). Also when the larvae mine in wrong directions they die before pupation (fig. 23g, h). When a particular floating leaf is affected by various larvae of *H. livens*, the leaf becomes too much damaged causing a faster rate of decomposition. The larvae, which have not reached the petiole in time drown, die because of lack of fresh plant tissue, or become infected by fungi. When too many larvae reach a particular petiole and consume too much tissue the leaf stalk easily breaks off or decomposes too fast. Then only the larvae which arrived first in the petioles, and which have eaten themselves a longer way downwards survive.

An important factor of mortality is the intraspecific competition especially at the end of the season when the number of larvae is maximal and more larvae mine in the same floating leaf.

In the last week of August, 1977, 25 floating leaves of *Nuphar* which were affected by *H. livens* larvae were gathered in the Oude Waal; the mean number of mine tracks per floating leaf was four. At the end of September, 1977, 25 leaf stalks of affected leaves were gathered and in them 1—3 pupae were found with a mean number per leaf stalk of two. So in 1977 about 50% of the larvae of the last generation did pupate, while apparently the other 50% died because of competition, especially with the older larvae. On 11 September, 1979, the mean number of mine galleries per floating leaf was 6 (maximum 15) (34 affected leaves from the Oude Waal were examined). On 15 October, 1979, 20 leaf stalks were gathered and in them 32 pupae were found. The maximum number of pupae per petiole was three, while the mean number per leaf stalk was 1.6. Therefore, in 1979 less than 1/3 of the larval population of the third generation in the Oude Waal pupated.

It can be concluded that the petiole offers room to 1—3 pupae only. Schütte (1921) recorded that the mine tracks of the larvae in the triangular petioles are mostly situated in their edges, using the space optimally in this way.

Pupation

According to Schütte (1921) the metamorphosis of summer larvae into summer pupae takes only a short time; transitional stages were never found. The metamorphosis of larvae into winter pupae, however, takes a period of at least 8—10 days.

The process of metamorphosis starts after the 4th moulting period. Just before pupation the larvae excrete calcium carbonate via their digestive tracks and originating from the Malpighian organs. A clod of calcium carbonate can be found near the caudal parts of the pupae in the petioles (fig. 24).

During the pupation of the winter generation the skin becomes ca. 9 times thicker by the formation of chitinous layers; furthermore calcium and silicium are chemically bound to chitine and thus incorporated in the pupal skin (Schütte, 1921).

The pupa

Morphological description

The pupae which emerge within the growing season of *Nuphar*, according to Schütte (1921) and Eberle (1943) summer pupae (in the Oude Waal and Haarsteegse Wiel the first and second generation), measure 7.0—8.3 mm in length
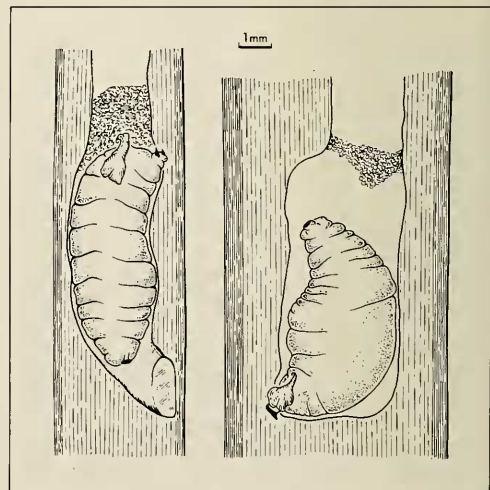

Fig. 24. Positions of a summer and a winter pupa in the petioles of *Nuphar* leaves (Eberle, 1943).

with a width of 2.6—3.3 mm (n = 10). Their pupal skin is rather soft, yellow-brown in colour and more or less translucent so that the developing adult is to be seen. The cylindrical body mostly consists of 12 clearly visible segments, while a large amount of minor chitinous projections on the pupal skin gives it a faintly, transversally striated appearance. The kidney-shaped frontal stigmata and the acute projections of the terminal stigmata are brown-black in colour and thus can be easily recognized.

The pupae of the third generation, according to Schütte (1921) and Eberle (1943) winter pupae, which hibernate during the winter, measure 6.2—7.2 mm in length at a width of 3.4—4.1 mm, so they are shorter but more robust than those of the first and second generations (fig. 24). The pupal skin is stout, yellow-brown to brown-black in colour and not translucent. The thick-set body, on which the 12 segments are not all clearly visible, has on its dorsal side a more or less visible yellow-brown line running from the kidney-shaped anterior stigmata to the large, dark-brown, acute projections of the terminal stigmata. The skin is also faintly transversally striated (fig. 25).

In the summer pupae the thoracic stigmata are in connection with the anterior stigmata of the pupal skin. This is not the case in the winter pupae; here the anterior stigmata of the pupal skin are in connection with a well-developed air layer, ca. two times as large in the winter pupae as in the summer pupae (Schütte, 1921).

Position of the pupae in the leaf stalks

Eberle (1943) already described that the pupae of the first generation have an other position in the petiole than the pupae which have to hibernate (fig. 24). The pupa which emerges within the growing season of *Nuphar* (the first and second generation in our case) is situated in a small room in the leaf stalk with its rostral end below and its caudal end above. This rostral end faces the window, the provision for the emergence of the adult, while the acute projections of the terminal stigmata are stuck into the living tissue of the leaf stalk. The room in which the pupa matures is closed off from the remainder of the mine gallery by a plug of loosened plant cells.

The pupa of the last generation (in our case the third one) is situated in a larger room in the petiole with its rostral end upward and its caudal end downward, so the other way round, when compared with the other generations. The

acute projections of the caudal stigmata are also stuck into the leaf stalk tissue. The broad room in the petiole in which the pupa occurs is often closed off by a small plug of loosened cells. As already mentioned this third generation has not made a window for emergence.

Emergence and hibernation

According to Schütte (1921) the pupal stage of the summer generation lasts 2—3 weeks. At the time of emergence the adult, originating from a pupa of the first or second generation, crawls out of the pupal skin and out of the leaf stalk via the window by means of its ptilinum. The new adult rises towards the water surface because its specific gravity is less than that of water.

The third generation hibernates as pupa and stays in the leaf stalk as long as possible until the petiole tissue has completely decomposed. During the decomposition of the leaf stalk, the pupa together with parts of the petiole, can sink towards the bottom of the pool, but when the petiole has decayed too much the pupa rises to the water surface. The pupal skin is partly filled with gas so that the pupa remains floating. In the Oude Waal floating pupae could not be found in autumn or the first part of the winter. In spring however a few of them were found between material washed ashore. Apparently the decomposition rate of the leaf stalks is not very fast; the pupae can stay a fairly long time in the petioles before they rise to the surface or wash ashore.

During the hibernation period a lot of pupae die; the spring generation is only very small, while in autumn most petioles of *Nuphar* contain pupae of *H. livens*. The solid pupal skin of the winter pupae has probably the function of protection against ice, predators or desiccation.

Summary and discussion

There are several relationships between the fly *H. livens* and the vegetation dominated by *Nuphar lutea*.

Adult *H. livens* visit the flowers of *Nuphar* for several reasons, viz.:

(a) collecting food in the form of nectar, furthermore preying in the flowers on soft skinned insects or on *Notiphila brunnipes* eggs;

(b) protection and shelter against bad weather conditions, e.g. heavy rain;

(c) resting site; the temperature in the flowers is higher than those of the surroundings during sunny weather conditions (table 3), which
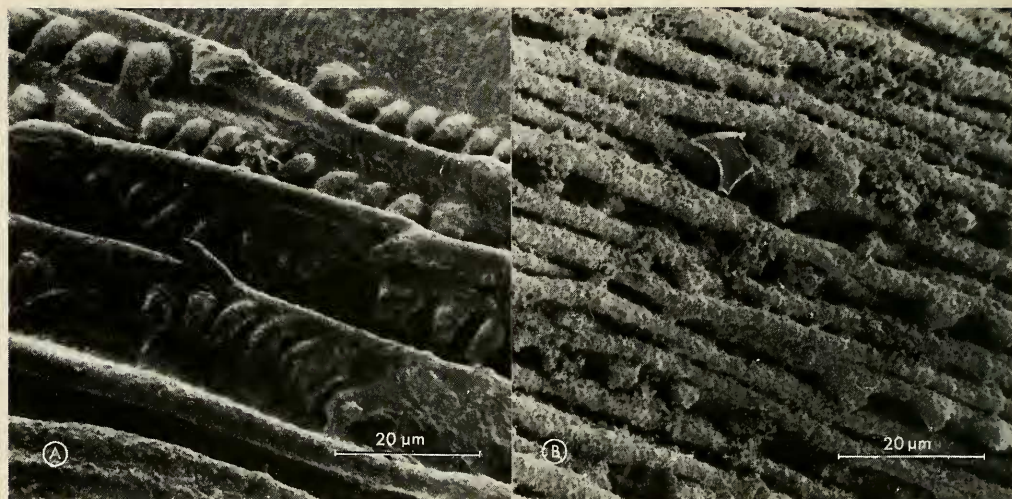
Fig. 25. Scanning electron microscope photographs of the skin of a summer (a) and a winter pupa (b).

probably is favourable for the flies (faster digestion and warming up of flight muscles);

(d) copulation site.

By their regular occurrence in the flowers and by their activities, the flies can cause pollination. In the areas investigated flowering of *Nuphar* took place from mid-June to mid-August so that predominantly the second generation of *H. livens* could visit *Nuphar* flowers.

Adult *H. livens* visit the nymphaeid floating leaves for:

(a) food; the fly preys here on Chironomidae and *Hydrellia* while the water drops occurring on the floating leaves are used for drinking;

(b) copulation site;

(c) egg deposition; oviposition takes place under the floating leaves of *Nuphar*;

(d) resting site, e.g. for sunning; the upper surface of the floating leaves can reach temperatures higher than those of the ambient air and water (table 3);

(e) shelter against bad weather conditions under aerial leaves of *Nuphar* and *Nymphaea* or leaf margins which have been curled up and dried out.

Because of their many activities on floating leaves, adults of *H. livens* might function as vectors of spores of parasitic fungi, which occur on the floating leaves such as *Glomerella cingulata* (Ston.) Spauld. et Schrenk. From mid-August till October decomposition of the nymphaeids exceeds production; at this time also the population of adult *H. livens* is at its maximum.

The eggs are deposited upon the underside of the floating leaf blades. An advantage of this kind of oviposition might be protection against desiccation and against predators such as adults of the own species or parasites.

The larvae and pupae of *H. livens* are bound to the floating leaves and petioles of *Nuphar*. The leaf blades and petioles function as:

(a) food; the larvae consume mesophyll and petiole tissue, creating mine galleries in this way;

(b) protection; the larvae and pupae are protected against possible predators in these mine galleries;

(c) oxygen supply; the larvae obtain oxygen from the intercellular cavities; the pupae thrust their caudal stigmata into the petiole tissue, obtaining oxygen in this way.

The consumption of living tissue by *H. livens* larvae initiates a decomposition process in the floating leaves of *Nuphar*. The tissue around the mine galleries very soon decays because of infection by fungi and bacteria. The comsumption and damage caused by *H. livens* in this way can amount to 5—10% of a floating leaf blade (Van der Velde, 1978), when the larval numbers have reached their maximum.

Parts of the leaf blades break off easily by wind and wave action on places where mine tracks of *H. livens* occur. Also the petioles break off easily on places where the larvae have pupated. In 1977, 15.3% of the floating leaves in the Haarsteegse Wiel and 11.7% of the leaves

Table 8. Comparison of the most important features of the life histories of *H. livens* and *H. confluens*.

	Hydromyza livens	*Hydromyza confluens*
Food plant(s)	*Nuphar lutea* (L.) Sm. *Nuphar pumila* (Timm) DC. *Nuphar × intermedia* Ledeb. (*Nuphar advena* Ait.)	*Nuphar advena* Ait.
Geographical distribution	Europe and Asia	North America
Number of generations	2—3	2 ?
Adults		
Food - on leaves	Chironomidae, *Hydrellia*	dead bodies of *Chironomus* ssp.
- in flowers	nectar, soft-skinned insects, *Notiphila* eggs	pollen ?, liquid substances
Pollinator	+	+
Spatial occurrence	more abundant on floating leaves bordering the open water	more abundant on floating leaves bordering the open water
Copulation site	flowers and floating leaves	flowers and floating leaves
Oviposition site	underside of leaf-blades of floating leaves	submerged petioles of floating leaves
Deposition of eggs	singly	singly
Air coat when going under water	+	+
Eggs		
Plastron	+ ?	?
Larvae		
Food	leaf- and petiole tissue	petiole tissue
Type of damage	mine gallery	interior excavation of petiole
Construction of window for emergence	+	+
Pupation site	in petiole	in petiole
Pupae		
Occurrence of summer pupae	+	+
Occurrence of winter pupae	+	?

in the Oude Waal separated and floated away, a process in which *H. livens* plays an important role.

These free floating parts of leaf blades and leaf stalks can have an important function elsewhere for other organisms for instance for the hydrozoan *Cordylophora caspia* (Pallas) (Roos, 1979).

From all these data it can be concluded, that the fly *H. livens* is an important element in the nymphaeid ecosystem dominated by *Nuphar*.

It appears from this study on *H. livens* and that of Welch (1914, 1917) on the North-American species *Hydromyza confluens* that the life-histories of both species in many ways resemble each other. The most important features of both *H. livens* and *H. confluens* are summarized in table 8.

Both flies have an important function in nymphaeid vegetation, *H. confluens* in stands dominated by *Nuphar advena* and *H. livens* in similar habitats dominated by European *Nuphar*

taxa. Furthermore, it is interesting that *H. livens* has the ability to affect the natural food plant of *H. confluens*. It is not known whether the larvae of *H. confluens* can also complete their life cycle on European *Nuphar* taxa. It should be mentioned that Beal (1956) considers *Nuphar lutea* (L.) Sm., *Nuphar pumila* (Timm) DC. and *Nuphar advena* Ait. to be subspecies of one species, viz. *Nuphar lutea*. Berg (1950) reports a normal development of a *H. confluens* pupa in the silty, humous bottom of a stream with respirating plates embedded in a root of *Potamogeton alpinus* Balb.

References

Beal, E. O., 1956. Taxonomic revision of the genus *Nuphar* Sm. of North America and Europe. — J. Elisha Mitchell Sci. Soc. 72: 317—346.

Berg, C. O., 1950. *Hydrellia* (Ephydridae) and some other acalyptrate Diptera reared from *Potamogeton*. — Ann. Ent. Soc. America 43: 374—398.

Brauer, F., 1883. Die Zweiflügler des Kaiserlichen Museums zu Wien III. Systematische Studien auf Grundlage der Dipteren-Larven nebst einer Zusammenstellung von Beispielen aus der Literatur über dieselben und Beschreibung neuer Formen. — Denkschr. mat.-naturwiss. Cl. K. Akad. Wiss. 47: 1—100, 5 pls.

Collin, J. E., 1958. A short synopsis of the British Scatophagidae (Diptera). — Trans. Soc. British Ent. 13: 37—56.

Eberle, G., 1943. Die Mummelfliege (*Hydromyza livens* Fall.). — Natur und Volk, Frankfurt am Main 73: 293—306.

Gaevskaya, N. S., 1966. The role of higher aquatic plants in the nutrition of the animals in fresh-water basins. Vol. 1: 1—232. — National Lending Library for Science and Technology. Boston Spa, Yorkshire, England.

Gercke, G., 1877. Ueber die Metamorphose der *Hydromyza livens* Fall. — Verh. Ver. naturwiss. Unterh. Hamburg (1879) 4: 229—234.

Grünberg, K., 1910. Diptera, Zweiflügler. Heft 2a. In: A. Brauer (ed.), Die Süsswasserfauna Deutschlands, eine Excursionsfauna: 1—312. — Gustav Fischer, Jena.

Hackman, W., 1956. The Scatophagidae (Dipt.) of Eastern Fennoscandia. — Fauna Fenn. 2: 1—67.

Hendel, F., 1928. Blattminenkunde Europas. I. Die Dipterenminen 2 (Bog. 5—7, pl. 3—5).

Hering, E. M., 1926. Die Ökologie der blattminierenden Insektenlarven. — Zoologische Bausteine, Ausschnitte aus dem Gesamtgebiet der Zoologie. Berlin 1 (2): 1—253.

Heslop-Harrison, Y., 1955. *Nuphar* Sm. Biological flora of the British Isles. — J. Ecol. 43: 342—364.

Hinton, H. E., 1960. How some insects, especially the egg stages avoid drowning when it rains. — Proc. S. Lond. ent. nat. Hist. Soc. 1960: 138—154.

——, 1967. The respiratory systems of the egg-shell of the common housefly. — J. Insect Physiol. 13: 647—651.

——, 1971. Polyphyletic evolution of respiratory systems of egg shells, with a discussion of structure and density-independent and density dependent selective pressures. In: V. H. Heywood (ed.), Scanning electron microscopy. Systematic and evolutionary applications. The Systematics Association Special Volume 4: 1—331 (pp. 17—36). — Academic Press.

De Meijere, J. H. C., 1895. Ueber zusammengesetzte Stigmen bei Dipterenlarven, nebst einem Beitrag zur Metamorphose von *Hydromyza livens*. — Tijdschr. Ent. 38: 65—100.

——, 1940. *Hydromyza livens* Fall. en *Notiphila brunnipes* Rob.-Desv., twee Dipteren, wier levenswijze verband houdt met *Nymphaea alba* L. — Ent. Ber. 10: 220—222.

Meusel, H., E. Jäger & E. Weinert, 1965. Vergleichende Chorologie der zentraleuropäischen Flora. Vol. 1: Text: 1—583. Vol. 2: Karten: 1—258. — Gustav Fischer Verlag. Jena.

Monchadskii, A. S., 1940 (according to Gaevskaya, 1966). (Diptera excluding Tendipedidae and Heleidae). In: V. I. Zhadin (ed.). Freshwater life in the USSR 1: 233—263. — Moscow Acad. USSR.

Roos, P. J., 1979. Two-stage life cycle of a *Cordylophora* population in the Netherlands. — Hydrobiologia 62: 231—239.

Sack, P., 1937. Cordyluridae. 62a. In: E. Lindner (ed.). Die Fliegen der palearktischen Region 7 (1): 1—103. — Stuttgart.

Séguy, E., 1934. Diptères (Brachycères) (Muscidae, Acalypterae et Scatophagidae). — Faune de France 28: 1—832 + pls. 1—27. Paris.

Schütte, L., 1921. Die Metamorphose von *Hydromyza livens*. Inaug. Diss., Greifswald: 1—48. — E. Hartmann, Greifswald.

Van der Velde, G., 1978. Structure and function of a nymphaeid-dominated system. — Proc. EWRS 5th Symp. on Aquatic Weeds (Amsterdam) 1978: 127—133.

——, 1980. Studies in nymphaeid-dominated systems with special emphasis on those dominated by *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Thesis Nijmegen, 163 pp.

—— & Th. C. M. Brock, 1980. The life history and habits of *Notiphila brunnipes* Robineau-Desvoidy (Diptera, Ephydridae), an autecological study on a fly associated with nymphaeid vegetations. — Tijdschr. Ent. 123: 105—127.

——, Th. C. M. Brock, M. Heine & P. M. P. M. Peeters, 1978. Flowers of Dutch Nymphaeaceae as a habitat for insects. — Acta Bot. Neerl. 27: 429—430.

Vockeroth, J. R., 1978. Scatomyzidae. In: J. Illies (ed.), Limnofauna Europaea. Eine Zusammenstellung aller die europäischen Binnengewässer bewohnenden mehrzelligen Tierarten mit Angaben über ihre Verbreitung und Ökologie. (2nd revised ed.): 1—532 (p. 489). — Gustav Fischer Verlag, Stuttgart, New York. Swets and Zeitlinger, Amsterdam.

Welch, P. S., 1914. Observations on the life history and habits of *Hydromyza confluens* Loew (Diptera). — Ann. Ent. Soc. America 7: 135—147.

——, 1917. Further studies on *Hydromyza confluens* Loew, (Diptera). — Ann. Ent. Soc. America 10: 35—45.

Wesenberg-Lund, C., 1943. Biologie der Süsswasserinsecten: 1—682. — Gyldendalske Boghandel Nordish Forlag, Kopenhagen und Verlag J. Springer, Berlin, Wien.